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THE ORIGIN OF INDIAN CORN AND ITS RELATIVES

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THE ORIGIN OF INDIAN CORN AND ITS RELATIVES

P. C. Mangelsdorf[1] and R. G. Reeves[2]

> **"The interest which surrounds an investigation into the history of a cultivated plant, increases with the importance of the uses to which the vegetable is applied, and the obscurity which prevails over the origin. There is a delight in probing within mysteries, and in the following out of clues which trace to mythology and the beginnings of things, especially when the value of the production lends a factitious dignity to everything connected with the investigation, and the fancy can play without the appearance of triviality, or the accusation of idle research."**
> **—E. Lewis Sturtevant, *Indian Corn,* (1879).**

Four hundred and forty-seven years ago, on November 5, 1492, two Spaniards whom Christopher Columbus had delegated to explore the interior of Cuba returned with a report of "a sort of grain they call maiz which was well tasted, bak'd, dry'd and made into flour." And so was introduced to the white man a plant which has since become, from the standpoint of total production, the second most important food plant in the world, a cereal treasure of immensely greater value than the spices which Columbus travelled so far to seek in his search for a westward route to India.

Today maize or Indian corn is grown in every state of the United States, in every suitable agricultural region on the globe; and a crop of corn is maturing somewhere in the world every month of the year. It grows from North Latitude 58° in Canada and Russia to South Latitude 40° in the Southern Hemisphere. Fields of maize are growing below sea-level in the Caspian Plain and at altitudes of more than 12,000 feet in the Peruvian Andes. Corn is cultivated in regions of less than ten inches of annual rainfall in the semi-arid plains of Russia and in regions with more than 200 inches of rain in the tropics of Hindustan. It thrives almost equally well in the short summers of Canada and the perpetual summer of tropical Colombia. No other crop is distributed over so large an area, and only one other, wheat, occupies a larger acreage. Today corn is grown on more than 200 million acres of land and produces an annual crop exceeding four billion bushels.

To thrive, or even to exist under such a wide variety of environmental conditions, a species usually must possess a great diversity of forms. This characteristic the corn plant exhibits to a degree probably not found in any other crop plant. The Russians have already collected more than 8,000 varieties and it is doubtful whether their collection is by any means complete.

Corn varieties differ from each other in many characteristics and by wide extremes. There are five main types—dent, flint, flour, sweet, and pop—which are distinguished by differences in the nature of the storage material in the grain. Superimposed upon this diversity in kernel type is

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a tremendous variability in numerous vegetative and other morphological characteristics. There are early-maturing varieties such as the Gaspé Flint from the Gaspé Peninsula in Canada, or Cinquantino from the Pyrenees Mountains of Spain, which mature in 60 to 70 days. There are very late varieties from Colombia that require ten or eleven months to reach maturity. The number of leaves varies from eight to forty-eight, the height of stalk from less than two feet to more than twenty, and the number of stalks produced by a single seed ranges from one to twelve. Size of ear varies from the diminutive ears of some of the pop corn varieties, which are no larger than a man's thumb, to the gigantic corn grown in the Jala Valley of Mexico, which produces ears measuring, with the shucks still attached, three feet in length, and stalks so tall that the ears may be harvested from horseback, and so stiff and strong that they are sometimes used for pickets in stockade enclosures for domestic animals (Kempton, 1924b).

In spite of this overwhelming diversity of form, all of the main types of corn known today were already being grown by the Indians when America was discovered and all of them are classified by botanists within a single species *Zea mays* L. Earlier botanists, it is true, have divided and subdivided the species into various subspecies but this practice has more recently been abandoned. All varieties of corn known today are readily hybridized with each other and the hybrids are, almost without exception, completely fertile. All evidence from botany, genetics, or cytology has, until recently at least, pointed to a common origin of all varieties of corn which exist today.

What was the nature of the wild or primitive corn from which our multitude of present varieties has developed? Where, when, and how was a species so hardy that it could survive in the wild converted to a cultivated plant so specialized and so dependent upon man's ministrations that it would soon disappear from the face of the earth if deprived of man's protection? These questions are all parts of one of the most intriguing puzzles of modern times, a puzzle which has occupied the attention of archaeologists who know that the ancient civilizations of Peru, Central America, and Mexico were based upon the culture of corn; ethnologists who know that corn played a prominent part in the religious beliefs and ceremonies of these ancient peoples, and was one of the chief motifs in their decorations; and botanists, geneticists, and cytologists who realize that a solution of this problem may throw revealing light upon evolutionary processes in general and expand still further our knowledge and understanding of the corn plant.

The problem has been attacked on many fronts, but, so far, no satisfactory solution has been found. There is no written historical evidence bearing on the problem previous to 1511. Maize is not mentioned in the Bible and in fact there was no Hebrew or Sanskrit term for maize. The Greek writers who discoursed intelligently and at length on other crop plants make no mention of maize. Evidently the Greeks had no word for it. There are no Egyptian representations of the plant or ear.

Extensive search of the pre-Columbian Chinese literature reveals no evidence that the Chinese scholars were acquainted with it. The records left by those ancient Americans—the Incas, Mayas, and Aztecs—tell us nothing of the origin of maize, though they do point out its importance in the economic, social, and religious life.

There are no fossil remains of maize. A single specimen from Peru believed to be a fossil several thousand years old, and resembling some of the Peruvian varieties of today, has been repeatedly cited as evidence of the great antiquity of maize. More recent examination of its petrographic nature has demonstrated that the so-called fossil is nothing more than an artifact, a clay rattle, perhaps a toy, devised for the amusement of some prehistoric infant.

In the absence of clear-cut evidence from history, archaeology, geology, or paleobotany, the only recourse is a study of the plant itself and its relatives. Such a study may take one of two main paths, comparative morphology or cytogenetics. Many competent studies have been made on the comparative morphology of maize and its relatives and though the facts disclosed by these have increased our knowledge of the resemblances and differences between maize and related species, and have told us something of the evolutionary paths it may have followed in attaining its present form, they have furnished little more than an occasional hint regarding the ancestry of the plant.

Genetic and cytological studies are more recent and though they have, so far, made no greater contribution toward a solution of the problem, they appear to us, in spite of what Weatherwax (1935) has termed the "limitations of the method" to provide the most promising avenue of attack; for it is rapidly becoming apparent that evolution is primarily a matter of gene change and chromatin rearrangement. If we can discover how the hereditary units, the genes, or the structures on which they are borne, the chromosomes, differ from each other and resemble each other in maize and its relatives, we may finally develop a picture of the common ancestor, or ancestors, and devise a satisfactory hypothesis to explain how the different species came into existence.

On this assumption and because the conditions in Texas, where the relatives of maize are readily grown out-of-doors, are particularly favorable for conducting such studies, we initiated some ten years ago a series of investigations on the comparative genetics and cytology of maize and its relatives. The results so far obtained have exceeded our most sanguine expectations. Though we cannot say that the problem has been solved and, indeed, it may never be completely solved, the new evidence recently brought to light has permitted us to develop new working hypotheses which are suggestive of promising new points of experimental attack on the problem.

Before presenting the results of our experiments it seems desirable to review the previous evidence on this problem, since only in the light of the many competent studies that have preceded are the new data capable of a satisfactory interpretation.

BOTANICAL RELATIONSHIPS OF MAIZE

Maize is a grass, though a most unusual one, as the early botanists clearly recognized. Its striking characteristics are quaintly, if not quite accurately, described by Lyte (cf. Dodoens 1578). "This Corne," he states, "is a marvellous strange plant, nothing resembling any other kind of grayne; for it bringeth forth his seede cleane contrarie from the place whereas the Floures grow, which is against the nature and kinds of all other plants, which bring forth their fruit there, whereas they have borne their Floure . . . at the highest of the stalkes, grow idle and barren eares, which bring forth nothing but the floures or blossomes . . ."

Within the family Gramineae, maize is assigned to the tribe Maydeae, more recently designated as the Tripsaceae (Hitchcock 1920), a tribe comprising eight genera, five of which are Oriental and three American. The Oriental genera which include Coix, Sclerachne, Polytoca, Chionachne, and Trilobachne are all native to the region extending from India and Burma through the East Indies into Australia. The chromosome number of these genera, so far as it has been determined, is usually ten, with the exception of one species of Coix, which has a chromosome number of five. Their resemblance to the American genera of the Maydeae is, in many respects, more superficial than real, and to this extent the tribe is an artificial one.

The American genera of the Maydeae are three. *Zea mays* L. the well known and widely grown Indian corn is so familiar to all Americans that it needs no further discussion at this point.

Euchlaena, commonly known as teosinte, comprises two species, annual teosinte, *Euchlaena mexicana* Schrad., and perennial teosinte, *Euchlaena perennis* Hitchc. The latter, however, is of questionable specific rank, and is known only in a single isolated locality in Mexico. It has twice the chromosome number of annual teosinte and is apparently an autotetraploid. This fact combined with its very limited distribution indicates that it is a comparatively recent development and as such it probably has no bearing on the origin of maize, though it has been very valuable for certain genetic and cytological studies.

Annual teosinte is undoubtedly the closest relative of maize. It has the same chromosome number, ten, and its chromosomes are homologous or partially homologous with those of maize. Except for short sections on several chromosomes, every chromosome of teosinte pairs closely and completely with a corresponding chromosome of maize and crossing-over between maize and teosinte chromosomes is, for most regions, approximately the same as in pure corn.

Teosinte occurs naturally as a weed in and around the corn fields in Mexico, and for years it was known only in that country. More recent explorations have shown that teosinte occurs in Guatemala so

Fig. 1. Plant of Florida teosinte grown in Texas from August planting. Teosinte blooms in Texas about October 15 regardless of time of planting.

thoroughly naturalized as to seem a part of the native flora, and that it is, in fact, the dominant species in parts of that country.

Tripsacum, the third American genus of the tribe, is represented by six species. The genus is in need of thorough monographic treatment by a competent taxonomist, but in the meantime the following species are recognized: *dactyloides*, *floridanum*, *lanceolatum*, *pilosum*, *laxum*, and

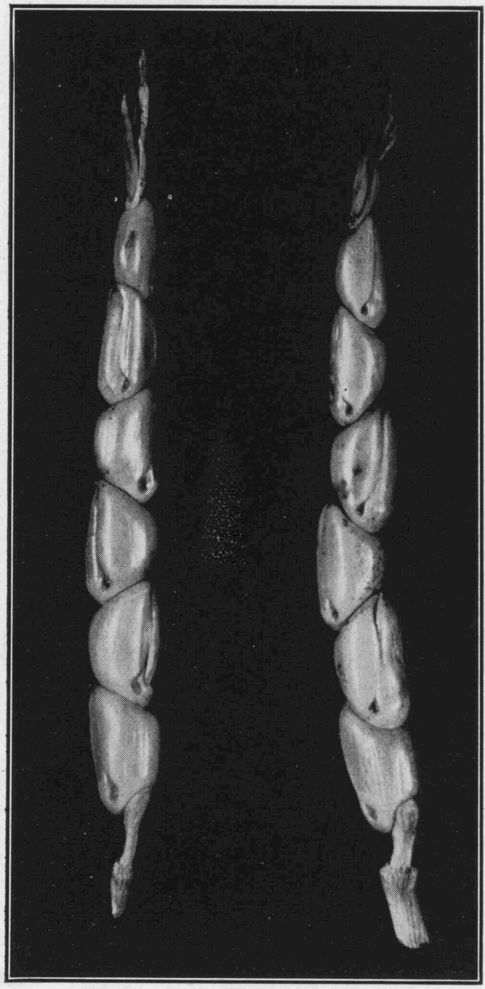

Fig. 2. Pistillate spikes of Florida teosinte. Note partially developed staminate spikelets at tips.

Fig. 3. Plant of *Tripsacum dactyloides* (Texas diploid).

latifolium. The last three species are tropical or semi-tropical and are found naturally only in Mexico and Central America. The first mentioned species, *T. dactyloides,* has the widest range of distribution, occurring almost throughout the Eastern half of the United States, from Texas to Massachusetts, and sporadically in Central and South America, and in the West Indies.

All of the species of Tripsacum are vigorous perennials and are known only in the wild, though a number of them have been, and are still being, tested as forage crops. The chromosome numbers of Tripsacum are 18 and 36. There is no marked visible effect from a doubling of the number. The diploid Tripsacum from Kansas, for example, resembles the tetraploid from Connecticut more closely than it does the diploid from Texas. Tripsacum does not cross naturally with maize but hybridization can be effected by a special technique which involves shortening of the styles or silks of maize and the use of enormous numbers of plants (cf. Mangelsdorf and Reeves 1931).

The conventional classification of the Maydeae is set forth below.

Botanical Classification of the Tribe Maydeae

It is generally recognized that the species here included in the genera Polytoca, Trilobachne, Sclerachne, Chionachne, and sometimes Coix, are close relatives, and many authors have placed the first four in a single genus. The Oriental Maydeae must be made the subject of further study before their affinities can be stated.

For further information on the synonomy and distribution of the groups, the reader is referred to Harshberger (1893), Sturtevant (1894), Nash (1909), and Hitchcock (1913, 1914, 1922a, b, 1927, 1930, 1935) for the American Maydeae, to Watt (1904) for Coix, and to Henrard (1931) for the remainder of the Oriental Maydeae. The notations given on the next few pages are not intended as complete descriptions; but, for the most part, are key characters used by many systematists. Obviously, we claim no originality for them.

Polytoca R. Br.

Inflorescence a modified panicle, one panicle terminating each long branch and several lateral ones arising in the axils of its uppermost leaves; the subtending leaves modified into spathes. Lateral panicles with usually one pistillate spikelet at base and five to ten staminate above, terminal panicle often staminate throughout. Spathes with laminas about as long to longer than the sheaths. Seeds protected by outer glumes, which are indurated.

P. wallichiana (Nees) Benth. *(Cyathorhachis wallichiana* Nees.) Fruit cases less than three times as long as broad; about 7 mm. long and 2.5 mm. broad, pubescent. Staminate spikelets 5-6 mm. long. Sikkim, Assam, Pegu.

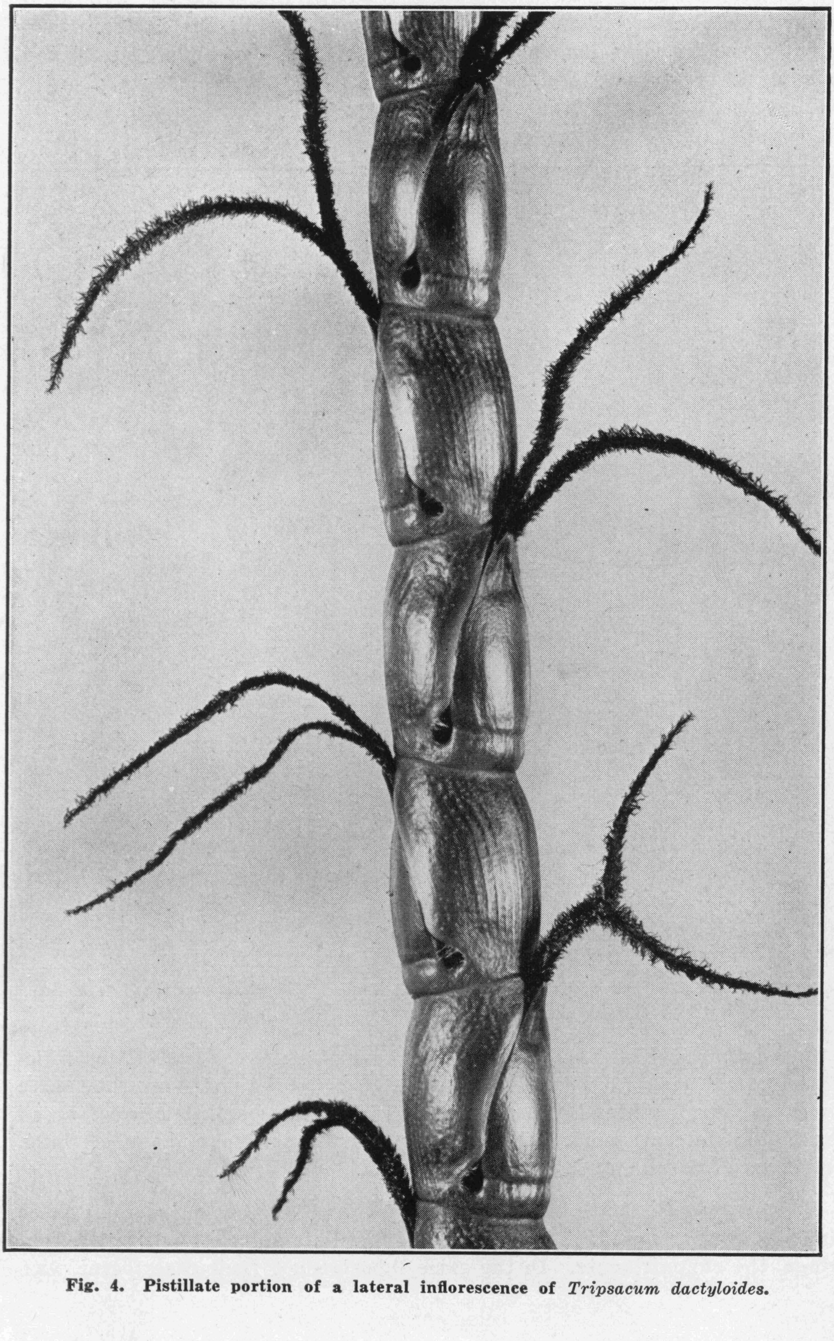

Fig. 4. Pistillate portion of a lateral inflorescence of *Tripsacum dactyloides.*

P. digitata (L.f.) Henrard (*Apluda digitata* L.f., *Polytoca heteroclita* Munro, *Coix heteroclita* Roxb., *Polytoca bracteata* R. Br.). Fruit cases about three times as long as broad; about 1 cm. long and 3 mm. broad, pubescent. Staminate spikelets 9-10 mm. long. British India, Tonkin, Philippines, Java, and Madoera.

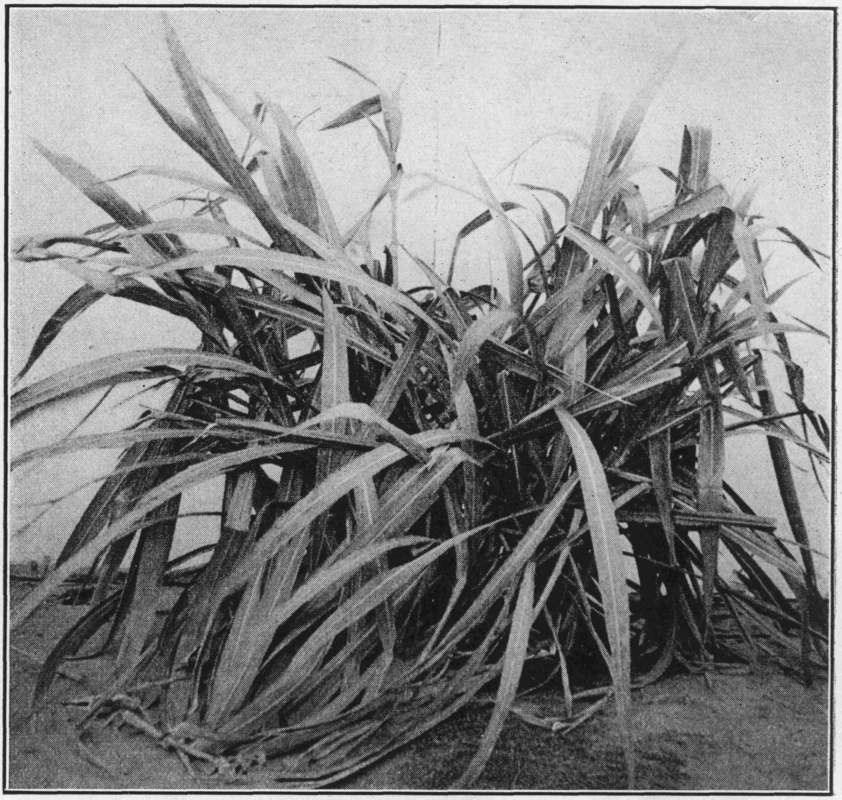

Fig. 5. Plant of *Tripsacum latifolium* grown in Texas. This plant was about to bloom in December when photograph was taken.

P. cyathopoda (Mueller) Bailey (*Sclerachne cyathopoda* Mueller, *Chionachne cyathopoda* Mueller). Fruit cases long and narrow, more than three times as long as broad. Lower glume of pistillate spikelets with broad expanding lateral wings, the summit blunt but emarginate or bifid. Northern Australia and Queensland.

P. macrophylla Benth. Fruit cases long and narrow, more than three times as long as broad. Lower glume of pistillate spikelets without lateral wings, the summit acute. In the same inflorescence fruit cases occur with one or two lateral teeth not reaching the summit. Malay Archipelago (Ternate), New Guinea (Kaiser Wilhelmsland), Bismarck Archipelago, Louisiade Archipelago.

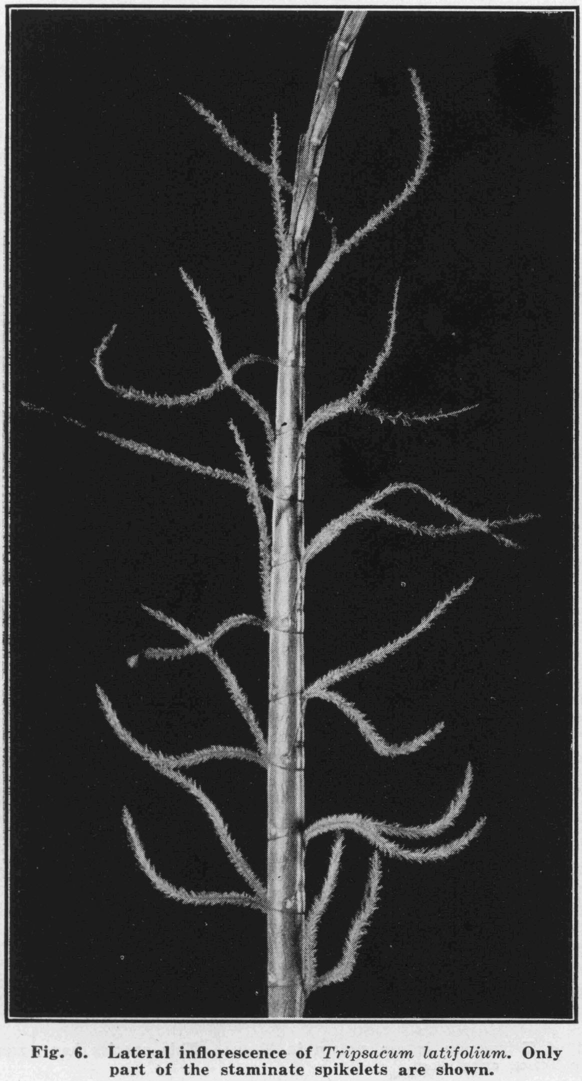

Fig. 6. Lateral inflorescence of *Tripsacum latifolium*. Only part of the staminate spikelets are shown.

P. barbata Stapf (*Coix koenigii* Spreng., *Coix arundinacea* Koenig, *Coix barbata* Roxb., *Chionachne barbata* R. Br., *Coix crypsoides* Mueller, *Chionachne koenigii* Thwaites). Fruit cases ovoid in outline, slightly

Fig. 7. Plant of *Tripsacum laxum* grown in Texas. This species has never bloomed under Texas conditions.

contracted below, rounded at the summit, without membranous wings, glabrous. British India, Tonkin, Ceylon, Celebes and Queensland.

***Trilobachne** Schenck

Differs from Polytoca by having the lower glume deeply three-lobed at the tip with the middle lobe largest, and a narrowly linear rather than an oval or puntiform hilum.

One species, *T. cookei* Schenck *(Polytoca cookei* Stapf), with the characters of the genus. British India.

Sclerachne R. Br.

Similar to Polytoca, except: all inflorescences usually bearing both staminate and pistillate spikelets; staminate spikelets only one to three; spathe slightly specialized, resembling a foliage leaf.

S. punctata R. Br., the only species. Characters of the genus. Java, Madoera, and Timbor.

Chionache R. Br.

Inflorescence only one, at the end of each branch of the culm; slender, spike-like. Five to seven pistillate spikelets in a dorsiventral row occupying the lower portion of the inflorescence, and 20 or more staminate spikelets above. Seeds protected by the indurated outer glumes.

Ch. biaurita Hackel. Fruit case very narrow, cuneiform; summit deeply cleft with two truncate, triangular membranous wings. Philippines, endemic.

Ch. semiteres (Benth.) Henrard *(Tripsacus semiteres* Wallich, *Polytoca semiteres* Benth., *Chionachne wightii* Munro). Fruit case narrowly cylindric, semiterete; margins of the lower glume ciliate at the middle, the apex not distinctly cleft. Deccan Peninsula and Burma.

Ch. sclerachne (Bailey) Bailey *(Polytoca sclerachne* Bailey). Fruit case ovate-lanceolate, strongly contracted at the summit; margins of the lower glume glabrous, the summit distinctly cleft with rounded lobes. Queensland, endemic.

Ch. massii Balansa *(Polytoca massii* Schenck). Differs from all of the preceding species in that the lower margins of the grain enclose a cavity at the bottom of which is found the hilum; hilum visible only from below, or partially from the front side. Tonkin.

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*This genus was proposed by Henrard (1931) largely on the basis of unpublished notes of the late Professor M. Schenck. We are uncertain whether the group should be given generic rank; but since Henrard's is the most complete classification available to us and since we have not studied Trilobachne at first-hand we are including it here as a separate genus.

Coix L. Job's Tears

This genus apparently is an assemblage of a few species and many varieties. The most comprehensive treatment of the group was published by Watt (1904), and his work has been found useful in the preparation of the present outline. Only one important departure is made here from Watt's treatment. He prefers to designate *C. aquatica* as a variety of *C. gigantea,* although he states that *C. aquatica* may have some claim to specific rank. Since *C. aquatica* is considered to be a species more often than not, and since the genus should be studied much more before a reclassification is made, we are following the customary practice of giving specific rank to three groups, *C. aquatica* Roxb., *C. gigantea* Koen., and *C. lachryma-jobi* L. There can be no doubt that intergrading forms exist, however.

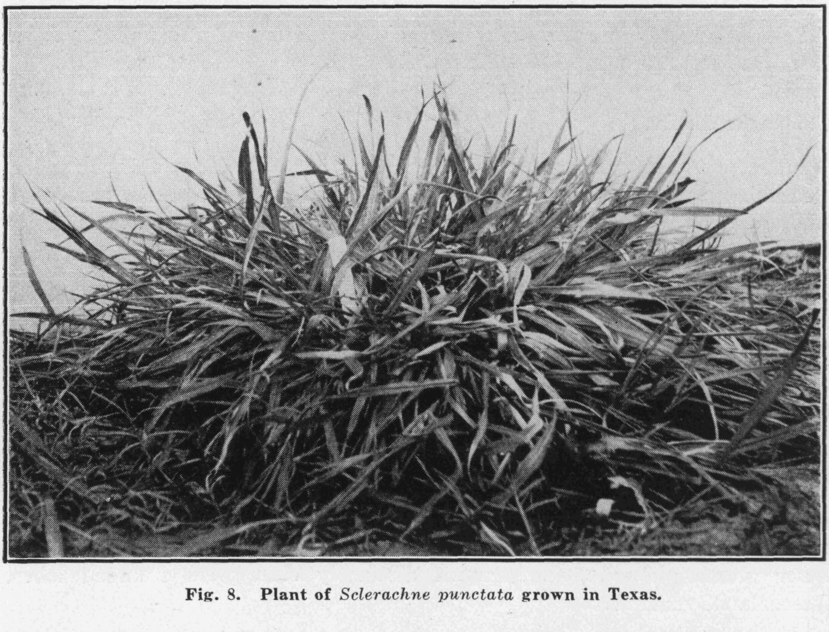


Fig. 8. Plant of *Sclerachne punctata* grown in Texas.

The genus may be characterized as follows: Inflorescences mostly lateral, branched at the base; each branch bearing one (sometimes two) indurated capsular spathes which completely enclose one functional pistillate spikelet and one or two rudiments, and the base of the rachis; upper portion of the infloresence bearing staminate spikelets, usually in sets of three. Outer glumes membranaceous.

C. gigantea Koen. *(Coix agrestis* Kunth, *Coix stigmatosa* Koch & Bouche, *Coix lingulata* Hack., *Coix lachryma-jobi* var. *gigantea* Hook.). Plant mesophytic. Stem perennial, erect. Leaves narrow, linear, shortly

Fig. 9. Plant of *Manisuris cylindrica*.

acuminate-lanceolate, glandular; union of blade with sheath a broad triangular suture projecting from either margin to the midrib; sheathes long, strongly ribbed. Capsular spathe pyriform; mouth only slightly prolonged, oblique, entire, thickened. Mature spathe flattened on one side with two longitudinal furrows; not constricted transversely. South India, Deccan, Bengal, United Provinces, Burma, Afghanistan, East Indies, Nagasaki, Yokohama.

C. aquatica Roxb. *(Coix gigantea* var. *aquatica* Watt). Plant floating or inhabiting swampy lands; large, often 20-100 feet long. Stem perennial. Leaves usually short, broad, ovate to linear-lanceolate, the glandular blade appearing to be a direct prolongation of the loose, open sheath; union of blade with sheath usually represented by a narrow line, but often possessing glands; sheaths strongly ribbed. Capsular spathe irregularly pyriform, apex drawn out into a tube that ends in a mouth obliquely prolonged into an acute lip. Mature spathe constricted transversely near the middle. Bombay, Bengal, Central Provinces, Burma, Shan States.

C. lachryma-jobi L. *(Coix lachryma* L., *Lithagrostis lachryma-jobi* Gaertn., *Sphaerium lachryma* Ktze.). Job's Tears. Annual or perennial mesophytes. Capsular spathe spherical to ovate-oblong, angular, only slightly drawn out at the apex; smoothly polished, very hard, usually bluish-white. Leaves glabrous, except for a double row of ascending teeth on the upper surface of each veinlet. Bengal, Himalaya, Assam, Central Provinces, Burma, Shan States.

Var. *stenocarpa* Stapf *(Coix stenocarpa* Balansa, *Coix tubulosa* Hack. & Warb.). Capsular spathe greatly elongated, bluish-white, and cut off abruptly at both extremities, becoming thin and straw-colored when the plants are grown under domestication. Burma, Shan States, Malaya, Polynesia.

Var. *monilifer* Watt *(Coix lachryma-jobi* var. *globosa* Tod., *Coix puellarum* Balansa). Capsular spathe usually broader than long, abruptly cut off or depressed at both extremities; mouth very large; chalky or milky-white to pink, brown, or black. Burma, Malaya, China, Japan.

This variety is peculiarly adapted to the making of ornamental beads, for which it is much used.

Var. *ma-yuen* Stapf *(Coix agrestis* Steud., *Coix chinensis* Tod., Balansa). Cultivated plants with edible fruits. Spathe thin, soft, striated, the basal portion usually constricted into an annulus or disk; of various colors except milky white. Bengal, Assam, Burma, China, Malaya. This variety contains an extensive series of cultivated forms.

The many varieties and forms of *Coix lachryma-jobi* are natives of India and China. However they have been introduced into numerous other countries because of their usefulness as cereals, medicinals, and ornamentals. Many forms that are regarded as intergrades between the varieties have been recognized.

Tripsacum L. **Gamagrass.**

This genus usually is distinguished from its American relatives on superficial examination by having well developed staminate and pistillate spikelets in all inflorescences, with the pistillate below, and from the Oriental genera by the almost complete absence of specialization of the upper leaf sheath into a spathe. Its forms are classified into various numbers of species, six usually being recognized. When the species and varieties of Tripsacum are more thoroughly known, a reclassification of the entire group may be desirable.

T. lanceolatum Rupr. (*Tripsacum acutiflorum* Fourn., *Tripsacum lemmoni* Vasey, *Tripsacum dactyloides* var. *lemmoni* Beal, *Tripsacum dactyloides hispidum* Hitchc.). Mexican Gamagrass. One of the spikelets of a pair nearly sessile, the other distinctly pedicelled; staminate spikelets membranaceous. Blades narrow, usually less than 12 mm. wide. Plants usually 1 to 1.5 m. tall. Huachuca mountains of Arizona south to Guatemala.

T. laxum Nash (*Tripsacum fasciculatum* Trin. Not *T. fasciculatum* Rasp.). Loose-panicled Gamagrass. One spikelet of a pair nearly sessile, the other with a pedicel 1 to 3 mm. long; spikelets soft, narrowed into a short point. Staminate inflorescence rather loose. Blades usually 5 to 7 cm. wide; plant tall and stout, as much as 2.8 m. high; sheaths glabrous. Southern Mexico and Central America.

T. pilosum Scribn. and Merr. Hispid Gamagrass. Differs from *T. laxum* by having hispid sheaths. Southwestern Mexico and Guatemala.

T. latifolium Hitchc. Guatemala Gamagrass. Both spikelets of each pair nearly sessile, abruptly rounded or obtuse at the summit, about 5 mm. long. Staminate inflorescence close. Blades mostly 3 to 6 cm. wide. Western Mexico and Central America.

T. dactyloides (L.) L. (*Coix dactyloides* L., *Coix angulatus* Mill., *Ischaemum glabrum* Walt., *Tripsacum monostachyum* Willd., *Tripsacum dactyloides* var. *monostachyon* Eaton & Wright, Wood, Gray, *Tripsacum compressum* Fourn., not *Tripsacum compressum* Rasp., *Dactyloides angulatum* Ktze., *Tripsacum dactyloides* var. *monostachyum* Vasey, *Dactyloides dactyloides* Ktze.). Eastern Gamagrass. Both spikelets of a pair nearly sessile; staminate spikelets indurated; terminal spikes usually more than one. Plants 1 to 2 m. tall; blades 1 to 2 cm. broad, flat. Conn. to Neb. south to the Gulf of Mexico, through tropical America to Brazil, Ecuador, Paraguay, and Bolivia; West Indies.

This species includes a number of forms that differ in morphological and cytological characters. It is in need of further study.

T. floridanum Porter (*Tripsacum dactyloides* var. *floridanum* Beal). Florida Gamagrass. Differs from *T. dactyloides* by being smaller and not so elaborately developed. Terminal spike usually solitary. Plant less than 1 m. tall. Blades 1 to 4 mm. wide, subinvolute. Southern Florida.

Euchlaena Schrad. **Teosinte**

This genus is readily separated from Zea, its nearest relative, by having a distichous pistillate inflorescence that disarticulates at maturity, and from Tripsacum by having the lateral inflorescences usually pistillate only and enclosed by subtending leaves. Two species usually are recognized, (1) *E. mexicana* Schrad. *(Reana giovanninii* Brign., *Reana luxurians* Durieu, *Euchlaena bourgaei* Fourn., *Euchlaena giovanninii* Fourn., *Euchlaena luxurians* Durieu & Asch., *Euchlaena mexicana* var. *luxurians* Haines), an annual, and (2) *E. perennis* Hitchc., a perennial. Both species are natives of Mexico, and *E. mexicana* also extends into Guatemala. Annual teosinte is cultivated for forage to some extent in the southern United States. Both species hybridize freely with Zea, and the hybrids of *E. mexicana* with Zea are approximately as fertile as either parent. Some varieties of *Zea mays* and *E. mexicana* each show characters of the other, as a result of their frequent hybridization. One variety of *E. mexicana*, called Florida Teosinte, shows fewer indications of hybridization than the Mexican varieties. Collins (1931) has pointed out that this variety would be regarded as a separate species if it were not that when it hybridizes with Zea, some of the segregates are indistinguishable from Mexican varieties.

Zea L. **Maize, Indian Corn**

The genus Zea usually is distinguished from its near relatives by having separate staminate and pistillate inflorescences, the staminate being terminal and the pistillate lateral, solitary, enclosed by subtending leaves; axis of pistillate inflorescence polystichous, not brittle, both spikelets of a pair usually developed.

The genus is monotypic, the one species generally being denoted as *Zea mays* L. The complete synonymy of this species is given by Harshberger (1893), Sturtevant (1894), and Hitchcock (1935).

Botanical History of the American Maydeae

Coix is the only one of the Oriental genera which has been considered as closely related to the American Maydeae. We have made numerous attempts to hybridize this genus with the three American genera, all without success, and we have finally dismissed the entire group with the conclusion that they have no immediate bearing on the problem of the origin of corn. It may become necessary to return to them later, though it appears to us that among the Old World grasses, both the sorghums and sugar cane offer more promise toward a solution of this problem than do any of the Oriental Maydeae.

Excluding, at least for the time, the Oriental genera of the Maydeae, because their relationship to maize appears to be remote, we have left for consideration in approaching this problem, three American genera, Zea, Euchlaena, and Tripsacum. It seems in order to review briefly at this point the botanical history of these three plants.

Maize: The first printed reference to maize and, incidentally, the first botanical description of this strange new plant appears in the famous "Decades" of Peter Martyre which were published in 1511.

The passage in which maize was mentioned, however, which appears in the first part of the first "Decade," was written, according to Laufer (1907), by November 1493, within one year after Columbus' discovery of America. Richard Eden in an English translation of the work under the title "Decades of the Newe Worlde or India," published in 1555, translates the passage as follows: "They make also an other kynde of breade of a certayne pulse, called Paniccm, much lyke unto wheate, whereof is great plentie in the dukedome of Mylane, Spayne, and Granatum. But that of this countrey is longer by a spanne, somewhat sharpe towarde the ende, and as bygge as a mannes arme in the brawne. The graynes whereof are sette in a marvelous order, and are in forme somwhat lyke a pease. While they be soure and unripe, they are white; but when they are ripe they be very blacke. When they are broken they be whyter than snowe. This kynde of grayne they call Maizium."

The first reference to maize in a botanical publication, according to Bonafous (1836), appears in 1532 in the "Stirpium" of Bock. Ruel mentions the plant in 1536. The first illustration, which is also one of the most artistic and accurate of the earlier ones, appears in the herbal of Leonard Fuchs, published in 1542. His drawings and descriptions are reproduced in Figs. 10 and 11. Fuchs (1542) gave the plant the name *Turcicum frumentum* or *Türckish korn* and this name and translated versions of it still persist in Germany and other European countries.

An attempt to list all of the published names that have been applied to maize is far beyond our intention, but some of the earlier names may be of interest.

When Columbus took maize to Europe on his return from America in 1493, he applied to it a modification of the Arawak name. Columbus called the plant *maiz,* but the Arawak name is *mà-hiz* or *marisi* (cf. Harshberger, 1893; Burtt-Davy, 1914). Since maize was taken to Europe before any attempt had been made to standardize the names of plants, one is not surprised to find that a profusion of names was in use, even in botanical works, within a few years. Most of the early works dealing with maize assign the plant Latin or Latinized names in accordance with the descriptions which also were written in Latin. In a few publications, however, we find the name of the plant given in the native language of the author. Any attempt to classify the early European names of maize as "botanical" and "vernacular" would lead to error, because no such distinction was in vogue and even the binomial system of nomenclature was not well established. By Peter Martyre in 1493, it was called *Panicum;* by Bock (Tragus) in 1539, *Wälschkorn;* by Fuchs in 1542, *Turcicum frumentum;* by Dodoens in 1552, *Milium indicum,* and in 1566,

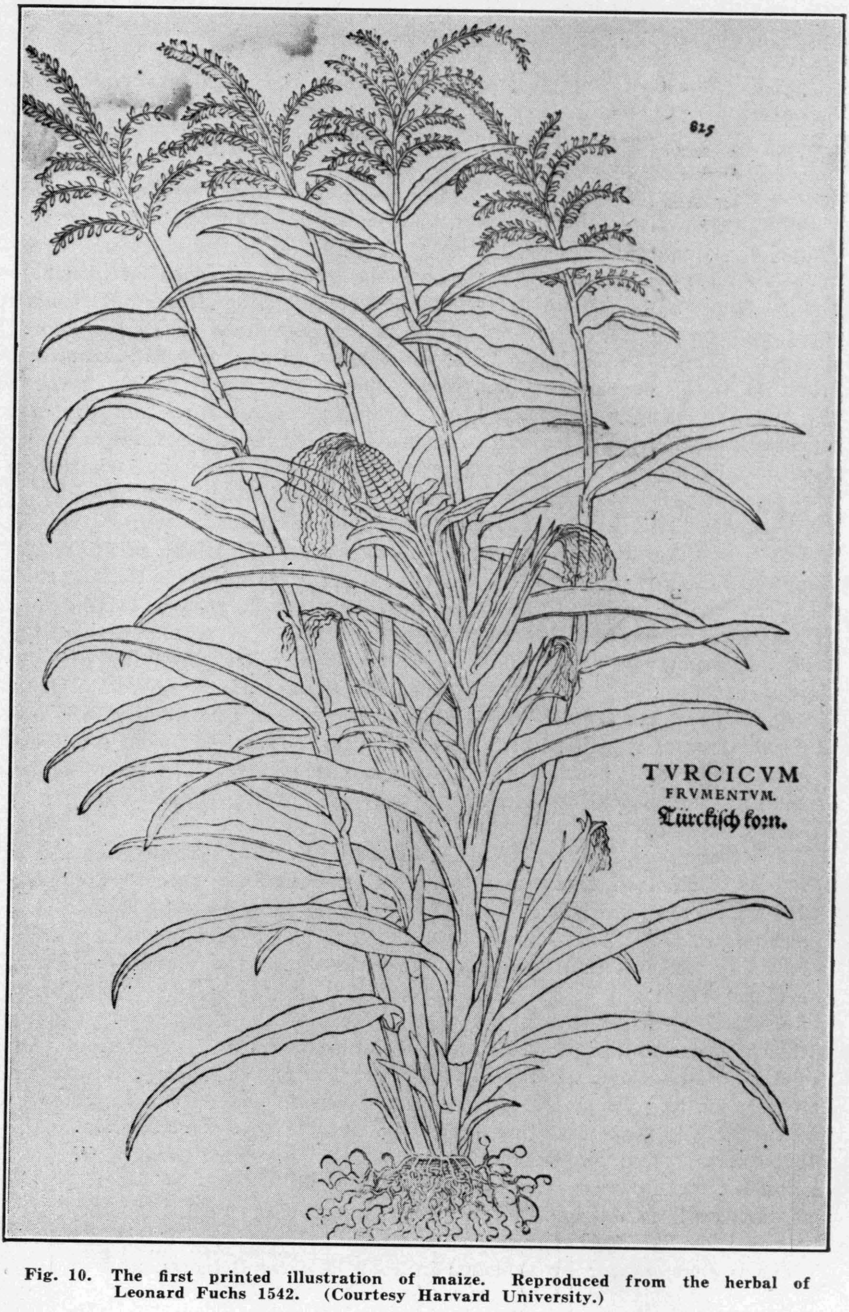
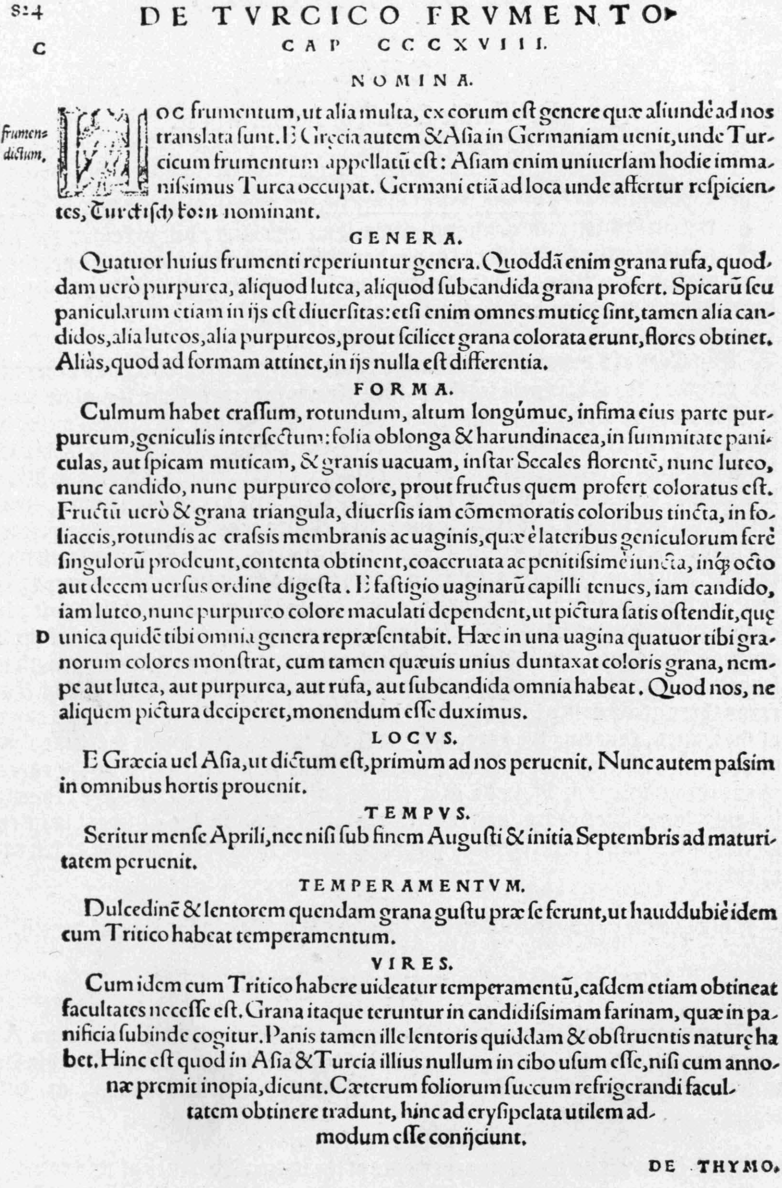


Fig. 10. The first printed illustration of maize. Reproduced from the herbal of Leonard Fuchs 1542. (Courtesy Harvard University.)



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DE TVRCICO FRVMENTO

C

CAP CCCXVIII.

NOMINA.

Turcicũ frumentum cur dictum.

Hoc frumentum, ut alia multa, ex eorum eſt genere quæ aliundè ad nos tranſlata ſunt. E Græcia autem & Aſia in Germaniam uenit, unde Turcicum frumentum appellatũ eſt: Aſiam enim uniuerſam hodie immaniſsimus Turca occupat. Germani etiã ad loca unde affertur reſpicientes, Turckiſch korn nominant.

GENERA.

Quatuor huius frumenti reperiuntur genera. Quoddã enim grana rufa, quoddam uerò purpurea, aliquod lutea, aliquod ſubcandida grana profert. Spicarũ ſeu panicularum etiam in ijs eſt diuerſitas: etſi enim omnes muticę ſint, tamen alia candidos, alia luteos, alia purpureos, prout ſcilicet grana colorata erunt, flores obtinet. Aliàs, quod ad formam attinet, in ijs nulla eſt differentia.

FORMA.

Culmum habet craſſum, rotundum, altum longúmue, infima eius parte purpureum, geniculis interſectum: folia oblonga & harundinacea, in ſummitate paniculas, aut ſpicam muticam, & granis uacuam, inſtar Secales florentẽ, nunc luteo, nunc candido, nunc purpureo colore, prout fructus quem profert coloratus eſt. Fructũ uerò & grana triangula, diuerſis iam cõmemoratis coloribus tincta, in foliaceis, rotundis ac craſsis membranis ac uaginis, quæ è lateribus geniculorum ferè ſingulorũ prodeunt, contenta obtinent, coaceruata ac penitiſsimè iuncta, inq; octo aut decem uerſus ordine digeſta. E faſtigio uaginarũ capilli tenues, iam candido, iam luteo, nunc purpureo colore maculati dependent, ut pictura ſatis oſtendit, quę
D unica quidẽ tibi omnia genera repræſentabit. Hæc in una uagina quatuor tibi granorum colores monſtrat, cum tamen quæuis unius duntaxat coloris grana, nempe aut lutea, aut purpurea, aut rufa, aut ſubcandida omnia habeat. Quod nos, ne aliquem pictura deciperet, monendum eſſe duximus.

LOCVS.

E Græcia uel Aſia, ut dictum eſt, primùm ad nos peruenit. Nunc autem paſsim in omnibus hortis prouenit.

TEMPVS.

Seritur menſe Aprili, nec niſi ſub finem Auguſti & initia Septembris ad maturitatem peruenit.

TEMPERAMENTVM.

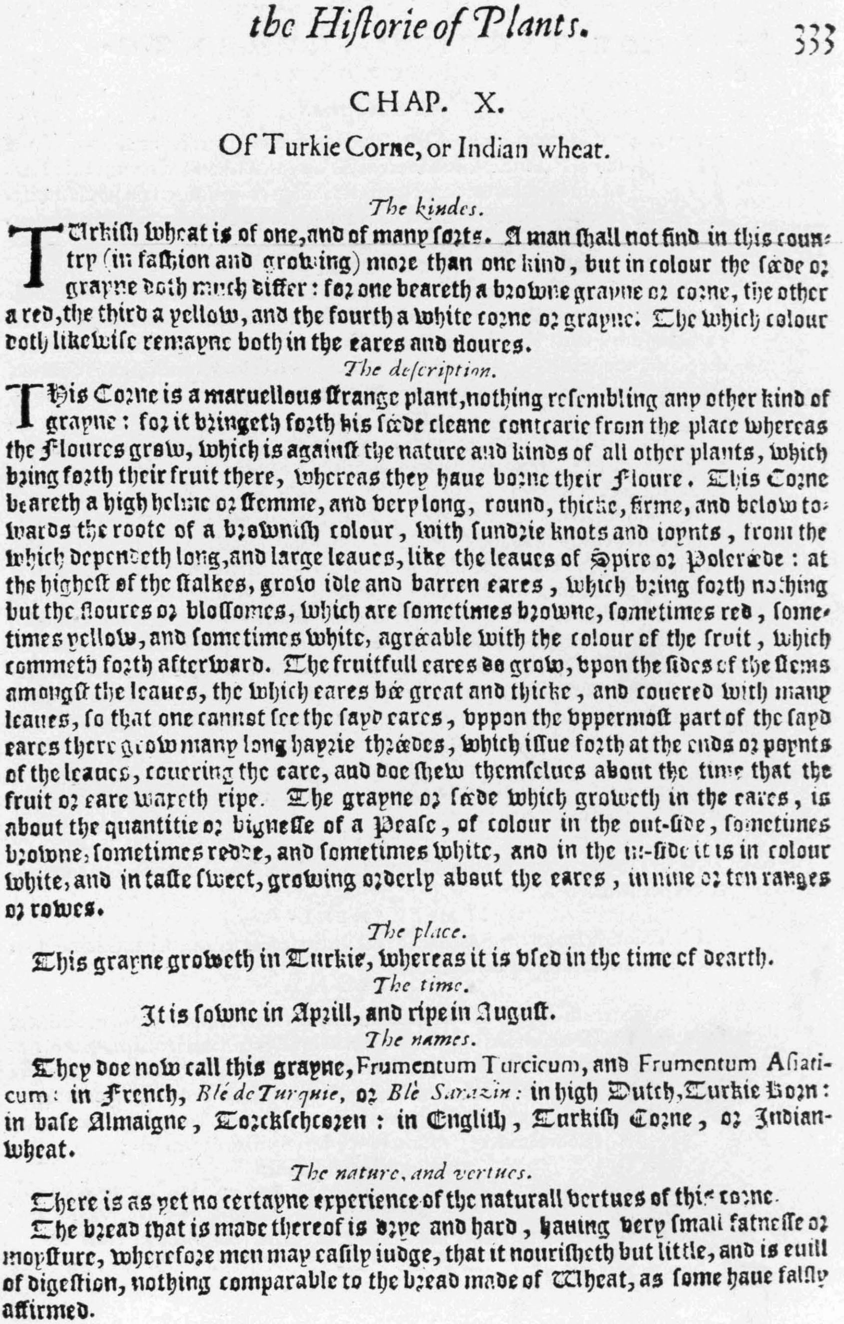
Dulcedinẽ & lentorem quendam grana guſtu præ ſe ferunt, ut hauddubiè idem cum Tritico habeat temperamentum.

VIRES.

Cum idem cum Tritico habere uideatur temperamentũ, eaſdem etiam obtineat facultates neceſſe eſt. Grana itaque teruntur in candidiſsimam farinam, quæ in panificia ſubinde cogitur. Panis tamen ille lentoris quiddam & obſtruentis naturę habet. Hinc eſt quod in Aſia & Turcia illius nullum in cibo uſum eſſe, niſi cum annonæ premit inopia, dicunt. Cæterum foliorum ſuccum refrigerandi facultatem obtinere tradunt, hinc ad eryſipelata utilem admodum eſſe conijciunt.

DE THYMO.

Fig. 11. One of the earliest botanical descriptions of maize. Reproduced from the herbal of Leonard Fuchs 1542. (Courtesy Harvard University.)



the Hiſtorie of Plants. 333

CHAP. X.

Of Turkie Corne, or Indian wheat.

The kindes.

Turkiſh wheat is of one, and of many ſoꝛts. A man ſhall not find in this country (in faſhion and growing) moꝛe than one kind, but in colour the ſœde oꝛ grayne doth much differ: foꝛ one beareth a bꝛowne grayne oꝛ coꝛne, the other a red, the third a yellow, and the fourth a white coꝛne oꝛ grayne. The which colour doth likewiſe remayne both in the eares and floures.

The deſcription.

This Coꝛne is a maruellous ſtrange plant, nothing reſembling any other kind of grayne: foꝛ it bꝛingeth foꝛth his ſœde cleane contrarie from the place whereas the Floures grow, which is againſt the nature and kinds of all other plants, which bꝛing foꝛth their fruit there, whereas they haue boꝛne their Floure. This Coꝛne beareth a high helme oꝛ ſtemme, and very long, round, thicke, firme, and below towards the roote of a bꝛowniſh colour, with ſundꝛie knots and ioynts, from the which dependeth long, and large leaues, like the leaues of Spire oꝛ Polerœde: at the higheſt of the ſtalkes, grow idle and barren eares, which bꝛing foꝛth nothing but the floures oꝛ bloſſomes, which are ſometimes bꝛowne, ſometimes red, ſometimes yellow, and ſometimes white, agrœable with the colour of the fruit, which commeth foꝛth afterward. The fruitfull eares do grow, vpon the ſides of the ſtems amongſt the leaues, the which eares bœ great and thicke, and couered with many leaues, ſo that one cannot ſee the ſayd eares, vppon the vppermoſt part of the ſayd eares there grow many long hayꝛie thꝛœdes, which iſſue foꝛth at the ends oꝛ poynts of the leaues, couering the eare, and doe ſhew themſelues about the time that the fruit oꝛ eare wareth ripe. The grayne oꝛ ſœde which groweth in the eares, is about the quantitie oꝛ bigneſſe of a Peaſe, of colour in the out-ſide, ſometimes bꝛowne, ſometimes redde, and ſometimes white, and in the in-ſide it is in colour white, and in taſte ſweet, growing oꝛderly about the eares, in nine oꝛ ten ranges oꝛ rowes.

The place.

This grayne groweth in Turkie, whereas it is vſed in the time of dearth.

The time.

It is ſowne in Apꝛill, and ripe in Auguſt.

The names.

They doe now call this grayne, Frumentum Turcicum, and Frumentum Aſiaticum: in French, *Blé de Turquie*, oꝛ *Blè Sarazin*: in high Dutch, Turkie Koꝛn: in baſe Almaigne, Toꝛckſchcoꝛen: in Engliſh, Turkiſh Coꝛne, oꝛ Indian-wheat.

The nature, and vertues.

There is as yet no certayne experience of the naturall vertues of this coꝛne.

The bꝛead that is made thereof is dꝛye and hard, hauing very ſmall fatneſſe oꝛ moyſture, wherefoꝛe men may eaſily iudge, that it nouriſheth but little, and is euill of digeſtion, nothing comparable to the bꝛead made of Wheat, as ſome haue falſly affirmed.

Fig. 12. Reproduction of Lytes' description of maize (cf. Dodoens 1578). (Courtesy Harvard University.)

Triticum frumentum; by C. Bauhin in 1623, *Frumentum indicum Mays dictum;* by Gerard in 1636, *Frumentum asiaticum;* by J. Bauhin in 1650, *Triticum indicum.* (cf. Bauhin 1623, Linnaeus 1753, Sturtevant 1899, 1919.)

It was assigned its present name *Zea mays** by Linnaeus in 1737, although the word ΖΑΩ meaning "I live" had earlier been used for other plants by the Greeks (cf. Bonafous 1836).

Concomitant with the wide diversity of names used by the early botanists was a marked disagreement on the question of whether maize was of American or Eurasian origin.

Sturtevant (1879) reviewed the literature published prior to 1879, and compiled imposing lists of names of prominent botanists who had favored the eastern and the western origin. Those who had concluded that maize is of eastern origin were: Bock, Ruellius, Fuchsius, Sismondi, Michaud, Gregory, Lonicer, Amoreux, Regnier, Viterbo, Donicer, Tabernaemontanus, Bonafous, St. John, de Turre, Daru, de Herbelot, and Klippart. The following considered it to be of American origin: Dodoens, Camerarius, Matthioli, Gerard, Ray, Parmentier, Discourlitz, de Candolle, Humboldt, Darwin, F. Unger, von Heer, de Jonnes, Targioni-Tozzetti, Hooker, Figuer, Nuttal, Mrs. Somerville, and Flint. The old beliefs that maize is of eastern origin were based principally upon a too great dependence on trivial names of plants and a few discoveries of fictitious objects of several kinds in the eastern hemisphere. Some of the arguments for an eastern origin are mentioned later.

Many of the early botanical descriptions of maize are more notable for their naïveté than for their accuracy; others are remarkably accurate considering the strangeness of the plant. The descriptions of Peter Martyre and Lyte have already been mentioned. The latter is reproduced in full in Fig. 12, and Parkinson's (1640) description is reproduced in Fig. 13. There is an interesting difference of opinion between Lyte and Parkinson with regard to the "vertues" of the grain, the latter insisting that it "giveth good nourishment to the body" while the former states that "The bread that is made thereof is drye and hard, having very small fatnesse or moysture, wherefore men may easily judge, that it nourisheth but little, and is evill of digestion, nothing comparable to the bread made of Wheat, as some have falsely affirmed."

The opinion expressed by Lyte has persisted in northern Europe until the present time to such an extent that there is still a decided prejudice in many countries against the use of Indian corn for human consumption.

Teosinte: The American Indians undoubtedly were familiar with Euchlaena, the nearest known relatives of maize, in pre-Columbian times, on account of the close resemblance of this plant to maize. The Aztec name *teocentle,* of which the name teosinte now in use is a modification, is commonly thought to signify "divine maize" or "God grass." Euchlaena

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*Linnaeus himself capitalized the specific name *mays,* and it is still capitalized by some writers. However, the decapitalized form now is in good usage, and is our preference.

1138 CHAP. 24. *Theatrum Botanicum.* TRIBE 12.

CHAP. XXIV.

Milium Indicum maximum Maiz dictum, ſive Frumentum Indicum, vel Turcicum aliquorum. *Indian* or *Turkie* Wheate.

AS a kinde of Millet although farre greater and differing notably from the former I muſt joyne this graine although ſome have made divers ſorts thereof, yet I cannot perceive any more then two ſpeciall differences, the one beareth eares at the joynts of the ſtalkes, the other at the tops following the flowers: the other differences conſiſt not in any other things then the colours, of the blooming firſt and of the graines afterwards.

1. *Maiz Frumentum Indicum vel Turcicum vulgare.* The uſuall *Indian* or *Turkie* Wheate.

This *Indian* Wheate ſhooteth from the roote which is thicke and buſhie, ſundry ſtrong and tall ſtalkes ſix or eight foote high, as thicke as a mans wreſt if it grow in any ranke ground, full of great joynts with a white pith in the middle of them, the leaves are long, twiſe as large and great as of Millet; at the toppes come forth many featherlike ſprigs, bending downewards like unto the toppe of Millet, which are either white or yellow or blew, as the graines in the eares will prove, which fall away, nothing appearing after them; but while they are in flower at the joynts of the ſtalkes with the leaves, from within two or three of the lower joynts up towards the toppes, come forth the eares one at a joynt wch have many leaves foulded over them ſmalleſt at the toppe, with a ſmall long buſh of threads or haires hanging downe at the ends, which when they are ripe are to bee cut off: which foulds of leaves being taken away, the head appeareth much like unto a long Cone or Pineapple, ſet with ſix or eight or ten rowes of Cornes, orderly and cloſely ſet together, each being almoſt as bigge as a Peaſe not fully round, but flat on the ſides that joyne one unto another, of the ſame colour on the outſide as the bloomings were, hard but brittle and eaſie to bee broken or ground, with a white meale within them ſomewhat dry and not clammy in the chewing. *Lobel* expreſſeth the figure of another ſort as he thinketh becauſe as hee ſaith it grew greater and higher, and the roote grew greater, and with more ſeparate tufts, the roote not differing in any thing elſe: but I thinke it no ſpecificall difference, not underſtanding by any that it is taken for another ſort, and therefore I have omitted it and ſpeake no more thereof.

1. *Milium Indicum maximum Maiz dictum ſive Frumentum Indicum vel Turcicum.* The uſuall *Indian* or *Turkie* Wheate.

2. *Frumentum Indicum alterum ſive minus.* The other leſſer *Indian* Wheate.

This other *Indian* Wheate is like the former both in ſtalkes and leaves, but not halfe ſo high or great, the eares likewiſe are not halfe ſo bigge, of as differing colours as it, but they doe not grow at the joynts of the ſtalkes as the other, but at the toppes following the flowers, which maketh a ſpecificall difference betweene them: the graine it ſelfe is being made into bread not of that nouriſhing qualitie that the greater ſort, is but weaker by much, nor is ſo ſtrong to breede ſo much blood as it.

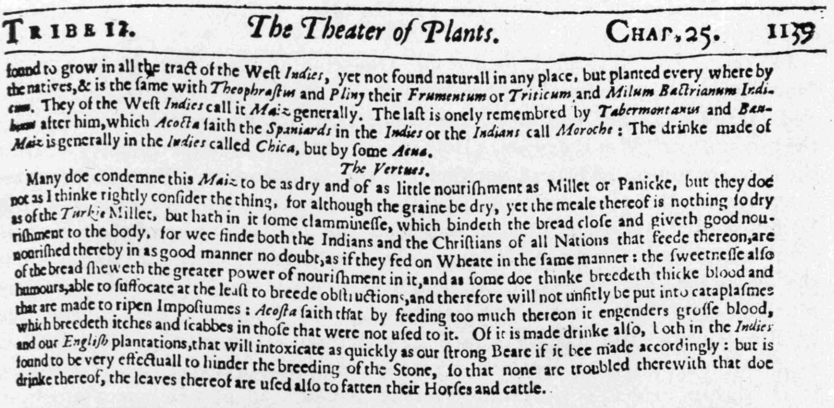
The Place and *Time.*

The firſt groweth in the Eaſt and Weſt *Indies*, and from both places have beene brought unto us, and have growne with us, and ſometimes borne ripe eares but not alwayes, and will deſire a ſtrong rich ground as the Millet doth, ſowne onely in the Spring and ripe in *September*: The other is a ſtranger, and ſeldome ſeene with us.

The Names.

It is very probable that this graine is that which *Theophraſtus* maketh mention of to grow in *Bactria*, which he ſaith was reported to be as bigge as Olive ſtones, and *Pliny* following him relateth the ſame thing out of him, but altereth the Olive ſtones into eares of Wheate, which ſheweth how ſubject it is to errour, to goe upon heareſay and bare report, for *Theophraſtus* relateth the greatneſſe of the graines but by report, which might increaſe by the way as it did betweene *Theophraſtus* and *Pliny* his time, to be as bigge as Wheate eares, *Matthiolus*, *Dodonæus*, *Lugdunenſis* and others condemne *Fuchſius* for calling it *Frumentum Turcicum*, according to his Countries dialect are found more juſt to be blamed themſelves, for no doubt but this very *Indian* Wheate which plentifully is

found



TRIBE 12. *The Theater of Plants.* CHAP. 25. 1139

found to grow in all the tract of the Weſt *Indies*, yet not found naturall in any place, but planted every where by the natives,& is the ſame with *Theophraſtus* and *Pliny* their *Frumentum* or *Triticum*, and *Milum Bactrianum Indicum*. They of the Weſt *Indies* call it *Maiz* generally. The laſt is onely remembred by *Tabermontanus* and *Bauhinus* after him, which *Acoſta* ſaith the *Spaniards* in the *Indies* or the *Indians* call *Moroche*: The drinke made of *Maiz* is generally in the *Indies* called *Chica*, but by ſome *Acua*.

The Vertues.

Many doe condemne this *Maiz* to be as dry and of as little nouriſhment as Millet or Panicke, but they doe not as I thinke rightly conſider the thing, for although the graine be dry, yet the meale thereof is nothing ſo dry as of the *Turkie* Millet, but hath in it ſome clammineſſe, which bindeth the bread cloſe and giveth good nouriſhment to the body, for wee finde both the Indians and the Chriſtians of all Nations that feede thereon, are nouriſhed thereby in as good manner no doubt, as if they fed on Wheate in the ſame manner: the ſweetneſſe alſo of the bread ſheweth the greater power of nouriſhment in it, and as ſome doe thinke breedeth thicke blood and humours, able to ſuffocate at the leaſt to breede obſtructions, and therefore will not unfitly be put into cataplaſmes that are made to ripen Impoſtumes: *Acoſta* ſaith that by feeding too much thereon it engenders groſſe blood, which breedeth itches and ſcabbes in thoſe that were not uſed to it. Of it is made drinke alſo, both in the *Indies* and our *Engliſh* plantations, that will intoxicate as quickly as our ſtrong Beare if it bee made accordingly: but is found to be very effectuall to hinder the breeding of the Stone, ſo that none are troubled therewith that doe drinke thereof, the leaves thereof are uſed alſo to fatten their Horſes and cattle.

Fig. 13. Reproduction of Parkinson's (1640) description of maize. The second form described may be the homozygous, earless form of pod corn. (Courtesy Harvard University.)

was used in religious ceremonies in early historical times. Numerous reports are on record of the Indians confusing Euchlaena with Tripsacum and thereby applying the name *teocentle* to Tripsacum. In other instances also, sometimes in localities where Euchlaena did not occur at all, Tripsacum was called *teocentle.* Thus it is probable that both plants were known by man previous to the time of written history of America.

The first permanent record of teosinte was published by Hernandez in 1790 who called it *cencocope* (cf. Kempton and Popenoe 1937). He used the names *teocintli* and *tepecentli* but applied them to some entirely different plant whose identity is not now definitely known. In 1832, Schrader published a botanical description of teosinte based on specimens which he grew from seeds sent from Mexico, and assigned it the botanical name in general use at the present time, *Euchlaena mexicana.* Rossignon sent seeds to France from Guatemala under the name *téozinté* in 1869, but the stock seems to have been lost, and as a result he sent another consignment of two different species called *téozinté* in 1875. There are records of other early introductions to other parts of Europe from Mexico, but it is usually believed that the cultivated Florida teosinte is derived from the introductions into France from Guatemala by Rossignon, since the original teosinte grown in Florida was introduced from France.

When Rossignon sent teosinte seeds to France, he gave Santa Rosa in southwestern Guatemala as the place of collection. Until recent years explorers who visited that locality expecting to collect teosinte were disappointed, and botanists began to think that teosinte had disappeared from Guatemala or that reports of its ever having grown wild there were erroneous. In the meantime, teosinte had been discovered in Mexico in several localities: around the city of Durango; near Chalco, State of Mexico; and at Guzman, State of Jalisco. However, all of the types found in Mexico differed from the Florida type. (Cf. Collins 1921, Kempton and Popenoe, 1937.)

In 1931, Dr. Wilson Popenoe of Guatemala City (cf. Collins 1932) found teosinte growing along the road near Jutiapa, in southern Guatemala, and stated that he had authentic reports of its occurrence elsewhere in that country. Weatherwax (1935) visited the Jutiapa locality during the dry season of 1932 and verified Popenoe's discovery. He also reported that the Indians of northern Guatemala were familiar with teosinte. Kempton and Popenoe (1937) explored for teosinte in various parts of Guatemala and southern Mexico. In southern Guatemala they found the so-called Florida type of teosinte, and in the northern part the Mexican type. On the ridge separating the Camojá Valley from that of Rio Huixta, and a little above San Antonio Huixta, they found thousands of acres where teosinte was the dominant vegetation. Therefore, it is highly probable that our Florida teosinte is of the same stock as that of southern Guatemala.

The variability of teosinte, the resemblance of some of its types to Tripsacum, and the uncertainty of the geographical distribution of certain types caused confusion among botanists until recent years. After Schrader described a Mexican form in 1832 as *Euchlaena mexicana,* thus establishing the new generic name Euchlaena, Brignoli in 1850 erected still another genus, Reana, for teosinte and called a form *R. giovannini.* It was thought that Brignoli's description was based upon the same form that Schrader had previously used, but Schumann (1904) states that Brignoli's studies were made "—zwar auf Grund einer Pflanze, deren Samen wiederum aus Centralamerika und zwar aus Mexico durch den D. D. Melchior Giovannini eingeführt worden war." In 1872 Durieu described teosinte grown from the seed sent to France from Guatemala by Rossignon in 1869, and assigned it the new specific name *R. luxurians.* Ascherson (1875, 1877, 1880) made careful studies of the morphology of the Mexican and Guatemalan teosintes and came to the conclusion that they were two species of the same genus, and that Schrader's generic name Euchlaena should be employed, since it had priority. Durieu became convinced that Ascherson's conclusions were correct, and as a result, he and Ascherson concurred in changing the name of Durieu's species to *Euchlaena luxurians* Dur. and Aschers. Still later *E. mexicana* and *E. luxurians* were seen to be so closely related that they could be no more than different races; therefore, *E. mexicana* Schrad., having priority, is now in general use. The published descriptions of *R. luxurians (E. luxurians)* fit the so-called Florida teosinte better than they do any of the Mexican forms, and since Florida teosinte is generally agreed to have come from stock traceable to France and thence to Guatemala, there is little doubt that Florida teosinte is the form originally called *Reana luxurians* Durieu.

Until the time of Ascherson's publications, Euchlaena was usually placed in the tribe Olyrae, but Ascherson showed convincingly that maize was its nearest known relative. He considered its taxonomic position to be between Zea and Tripsacum, and that view is often held at the present time. A. Braun (cf. Ascherson 1875) had previously demonstrated the relationship of Tripsacum and Zea to the Andropogoneae. Thus our present conception of the taxonomic position of maize and its relatives came into existence.

Tripsacum: The earliest record of Tripsacum in the scientific literature, of which we have been able to find any mention, is that of its being described and named *Gramen Dactylon maximum americanum* by Plukentius some time previous to 1753 (cf. Linnaeus 1753). Linnaeus himself called it *Coix dactyloides*, and later, in 1759, (cf. Hitchcock 1935) changed this name to *Tripsacum dactyloides.* These facts apply only to one of the recognized species, but this was the first species of Tripsacum to find its way into botanical literature and is the most widely distributed of them. During the years following, several new species were described, and new names proposed for those already known. Except for these studies, and several contributions to our knowledge of its distribution and habitat, no botanical studies of Tripsacum were reported until relatively recent years. The early taxonomic studies, of course, were based entirely on external gross morphology. The relationship of Tripsacum to Zea was pointed out by A. Braun, however, previous to the recognition of the affinity of Euchlaena to Zea (cf. Ascherson 1875).

Recognition of the Relationship of Zea, Tripsacum, and Euchlaena

It is obvious in reviewing the botanical history of the American Maydeae that for many years after maize and its two nearest relatives were discovered, named, and described, very little effort was made on the part of botanists to determine how the three species came into existence. It is true that both Tripsacum and teosinte were known to occur in America; but maize, the most interesting of the three, was unknown in the wild state and its relationship to its relatives was very obscure. One may think that botanists would have eagerly sought the origin, botanical as well as geographical, of any plant as unique and interesting as maize. A glance at the history of botany from the time of the discovery of America until 1860 will be required to make the reason clear.

It may be recalled that America, and therefore maize, was discovered approximately at the beginning of the Modern Age. The world was then emerging from a period during which civilization in general was at a low ebb, and natural science was no more advanced than the ancient Greeks and Romans had left it, if indeed as much so. But the period into which man was entering was one of renewed interest in intellectual subjects, and during it the herbalists were the principal contributors to the knowledge of botany. The earliest herbalists studied plants almost exclusively from the standpoint of *Materia Medica,* regarding them merely as vehicles of medicinal value. Classification was based upon the general impression that the plant made upon the observer rather than upon definite characters. However, the herbalists did usually write their descriptions from the plants themselves rather than copy the descriptions of their predecessors, as had been done for many previous centuries. Bauhin, often considered the last of the herbalists, seems to have had a vague impression that plants were related, but he stated no sound principle of classification. However, he did sum up all of the best knowledge of plants and attempted to put an end to the practice of giving each species a large number of names. The duration of this period was roughly from 1530 to 1623.

The period following that of the herbalists was distinguished by the classification of plants according to their differences, and by specific characters. Botanists of this period advocated the classification of plants according to natural affinities, but, paradoxically, most of them held to the dogma of the constancy of species and believed that each type represented an idea of the Creator. This school ended about 1760 with Linnaeus although some botanical historians consider that Linnaeus was among the first botanists of the succeeding period.

The next period of nearly a century saw many advances in our knowledge of plants; for during that time came the notable works of the de Jussieus, the Gartners, the de Candolles, Robert Brown, Endlicher, Lindley, Brongniart, Grew, Malpighi, von Mohl, and many others; however, not until immediately after this period, with Darwin, did the idea of mutability of species come into prominence.

Thus a long period of time elapsed after the discovery of maize before many biologists had even the conception of relationships of plants that would be required for them to consider the problem of phylogenetical or botanical origin. And it is also for this reason that many years elapsed before the botanical relationships of maize, teosinte, and Tripsacum became a problem.

PREVIOUS EVIDENCE ON THE ORIGIN OF MAIZE

Historical Evidence

The earliest written record of maize according to Sturtevant (1919) appears in the Popol Vuh, the sacred book of the Quiché Indians of Western Guatemala, whose records extend back to the eighth century. In this book is recorded a legend of four barbarians who guided the Quichés to "A most excellent land, so full of good things, where the white and yellow maize did abound . . ." Obviously this legend supplies but very little evidence upon the origin of maize except to suggest that it did not originate in western Guatemala.

Later historical evidence bearing on the origin of maize falls into two distinct categories: (1) Pre-Columbian Old World evidence, which by virtue of the conspicuous and consistent absence of any reference to maize provides convincing testimony of its New World origin; (2) Post-Columbian evidence, which shows the widespread distribution of maize in America at the time of the Discovery and thus suggests its great antiquity as a cultivated plant in America.

Maize is not mentioned in a single Old World treatise previous to the year 1492, although there are numerous records in which it certainly would have been discussed had it been known.

It is not mentioned in the Bible, and in fact there was no Hebrew word for maize. The Vedic bards who composed the Rig-Veda and other Vedas were obviously not acquainted with the maize plant, and possessed in their vocabulary no Sanskrit word for maize. There are no Egyptian representations of the plant or ear, although other crop plants and domestic animals were commonly depicted by the ancient Egyptians. Pliny, it is true, lists Zea as among the plants grown in Egypt, but he was undoubtedly speaking of one of the species of wheat to which this name was applied by the early Greek botanists (cf. Woenig 1886.) At any rate, no authentic specimens of the grain or ear have ever been discovered either in the tombs or pyramids of ancient Egypt or the ruins of Assyria and Babylonia. The specimen found by Rifaud in a tomb at Thebes is now generally conceded to have been the work of an impostor, and the famous charter of Incisa of 1204 according to which seeds of maize were brought from Anatolia by the crusaders has been shown to be a fabrication (cf. East 1913).

The Greek writers on agriculture, of whom there were many, at least 40 or 50 according to the later Roman writers Columella and Varro (cf. Dickson 1783), and who discussed the Old World plants intelligently and at length, made no mention of maize. Nor is it mentioned by any of the Roman writers: Pliny, Cato, Varro, Virgil, Columella, and Palladius, all of whom discoursed on agricultural subjects.

The Portuguese voyagers to Africa and Asia in the period immediately preceding the discovery of America apparently never encountered maize; or if so, they passed on to others no account of their discovery.

The *Ortus Sanitatus* of 1491, which preceded America's discovery by only one year, is lacking in any reference to maize (cf. Anon. 1853).

The only historical evidence which has been seriously considered as suggesting an Old World origin of maize is the reference in the famous *Pên ts'ao kang mu* of Li Shih-Chên, who was the greatest Chinese authority of his time on natural history. It was this passage which led Bonafous (1836), who assumed that the book had been written early in the sixteenth century, to conclude that maize had a Chinese origin. De Candolle (1855) and later writers have shown, however, that this treatise was probably written at a much later date than Bonafous had supposed.

The post-Columbian history of maize is voluminous but the essential facts are relatively few. The first Europeans to be introduced to maize, as has already been mentioned, were two Spaniards whom Columbus had delegated to explore the interior of Cuba and who returned to him on November 5, 1492 with a report of "a sort of grain they call maiz" (Churchill 1732).

The first printed reference to maize, as has also been mentioned, is that in the "Decades" of Peter Martyre, published in 1511 but written in 1493 (cf. Laufer 1907).

According to Benzoni who wrote in 1572, Columbus is said to have brought maize from America on his return to Spain, along with parrots and other new Indian articles (cf. Sturtevant 1919). Columbus in his letter to Ferdinand and Isabella, dated May 30, 1498, writes of the use of maize in the New World and in another letter speaking of his brother states: "During a journey in the interior he found a dense population entirely agricultural, and at one place passed through eighteen miles of corn fields" (Harshberger 1893).

Later explorers to the New World found maize being grown by the Indians in almost all parts of America from Canada to Patagonia. Cartier found it growing near Montreal in 1535.* Champlain noted cultivated fields of corn in 1605 at the mouth of the Kennebec River in Maine and also at Cape Cod. The Puritans who landed in New England in 1620 were carried through their first long, dreary winter by corn obtained from the Indians, and took their first lessons in corn culture the following spring. Hendrik Hudson bought ears of corn, pumpkins, and tobacco when anchored off the Catskills in 1609. The Swedish settlements in New Jersey and Pennsylvania purchased maize for sowing and for food. Corn was found growing around the James River in 1607, and the colonists sent over by the London Company took lessons in its culture. Cabeza de Vaca and De Soto found corn in Florida; the former in Texas as well. Marquette encountered it in the Mississippi Valley and La Salle in the region of the Great Lakes. Cordova found corn in Yucatan, Cortez in Mexico, Nuñez in Guiana, Gonzalo Ximenez in New Granada (Colombia), and Pizarro in Peru.

Everywhere in America, in fact, where agriculture was practiced maize was the basic food plant and almost everywhere, too, it furnished the Europeans with a strong foothold in the New World, without which successful colonization would have been extremely difficult if not almost impossible.

The spread of maize into the Old World was extremely rapid. Within one generation it was known over most of Europe. Within two generations, probably not later than 1540, it had reached China from the west through Tibet from India, to which the Spanish or Portuguese traders had carried it in the previous generation. By the time that European ships were touching the Chinese coast, maize was extensively grown and was already being taxed by the Emperor, which shows not only how rapidly it spread but also how quickly governments recognize new sources of taxation. Laufer (1907), to whom we are indebted for the facts regarding the introduction of maize into China, was greatly impressed by the rapidity with which it occupied new regions. He states: "Of all the manifold gifts of the New World maize spread the most rapidly†—travelled with

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*These accounts are taken from the numerous papers of Sturtevant and from Harshberger (1893) and Carrier (1923). We have made no attempt to verify the original references.

†Laufer was of the opinion that maize spread even more rapidly than syphilis, also an American introduction, but recent studies by Goodrich (1938) indicate that syphilis was first noted in China in 1505 and first recorded in 1545. The first reference to maize in the Chinese literature is assigned to the year 1573 by Goodrich.

much greater speed than the ships of the European nations which then shared in the universal trade, for long before the arrival of Europeans in China, maize was known there as an overland arrival, so that the idea of a European origin of it never struck the Chinese."

The rapid spread of maize throughout the Old World after the Discovery, the almost universal mention of maize by all the early explorers to America, and the complete absence of references to maize in the pre-Columbian Old World litrature—these three facts constitute perhaps the most convincing evidence of the American origin of maize. However, beyond establishing its nativity, the historical evidence tells but little about the origin of maize.

Possibility of a Pre-Columbian Old World Distribution

The evidence supporting the conclusion that maize is of American origin is almost overwhelming, and since the time of de Candolle (1855) the question of an Old World origin has seldom been seriously considered, although Grisebach (1884), writing in 1871, favored the Old World origin of maize because Coix, he said, was the nearest relative of maize and was native only to the Old World. He believed that no group of grasses related to maize had been found anywhere in America; and that maize had been taken to America through prehistoric contacts with Asia, in the same manner that he thought the higher cultures of Mexico and Peru to have been borrowed. The last doubts on this score, however, were removed when Ascherson (1875) demonstrated the close relationship of maize and teosinte.

The question of a pre-Columbian distribution in China has, however, been occasionally raised anew; in the last century by Siebold and Mayers (cf. Laufer 1907) and more recently by Collins (1909), who considered that the discovery in Chinese maize of a distinctive type of endosperm known as waxy, a type then unknown from any other part of the world, suggested a long period of maize culture in China. Since that time, however, waxy endosperm has been discovered in the Philippines by Weston (Collins 1920) and in both North and South America, in the former in New England (Mangelsdorf 1924) and in the latter in Argentina (Bregger 1928).

As a matter of fact Collins' question of a pre-Columbian distribution was answered before it was raised by Laufer's (1907) comprehensive studies on the introduction of maize into China. Laufer points out that maize is not described by any Chinese work previous to the *Pên ts'ao kang mu* of Li Shih-Chên. The passage in this work which is translated as stating that "the seeds of maize came from the western territory" must, according to Laufer, be interpreted as meaning that maize came from the western part of China, and he concluded that maize reached China from India through Tibet. Since the appearance of Laufer's paper, Swingle (cf. Collins 1919b) has made an extensive study of the pre-Columbian Chinese literature, which is rather voluminous, and has found no mention of maize. There has been no further development of a suggestion by Lacy (1911) that a certain reference to maize in the Persian literature may indicate a pre-Columbian Old World distribution. It is now generally agreed by all students of the problem that maize was confined to America before the Discovery. Merrill (1930, 1937) has concluded that the Old World and the New possessed in common before the Discovery, not a single cultivated plant except the bottle gourd, the fruit of which may have been widely disseminated by ocean currents.

Evidence from Geology and Paleobotany

Fossil remains, when they are available, constitute perhaps the most fruitful source of evidence in tracing evolutionary paths of plants and animals. Although paleobotanists are inclined to differ on the exact identity of some of the fossil grasses which have been uncovered, they are agreed that some of the fossils do represent true grasses, and the evidence indicates that the grasses were widely scattered and strongly developed in the Tertiary period and that many of our present-day genera were in existence at that time. From a study of the adaptations of the teeth of mammals, Osborn (1910) concluded that grasses attained their widespread distribution in both hemispheres toward the close of the Eocene. Elias (1935) in a recent critical summary of fossil grasses lists Arundo, Phragmites, and perhaps Bambusa as occurring in the Tertiary and several genera of the Agrostideae and Paniceae from the specific periods Miocene and Pliocene. Although Bambusa is generally regarded as one of the most primitive of grasses and Zea one of the most highly developed, the two may be more closely related than taxonomists have suspected, for both have recently been hybridized with Saccharum (Venkatraman 1938, Janaki Ammal 1938). Nevertheless there are no well authenticated instances of fossil remains of maize or of the other American Maydeae, Tripsacum and Euchlaena.

Darwin in 1846 (cf. Darwin 1868) reported having found heads of maize together with eighteen species of recent sea-shells embedded in a beach, then eighty-five feet above sea level, on the island of San Lorenzo off the Coast of Peru. As the result of this and other evidence, he concluded that maize had originated in that general region. Weatherwax (1935) has pointed out that this observation is of less significance than has sometimes been attached to it, for Darwin himself concluded that the deposit might have resulted from a tidal wave at a time when the surface was lower than today but still considerably above sea level. When we consider Darwin's unusual capabilities both as a biologist and geologist as well as his immense powers of observation, we are inclined to concur in his opinion that the maize ears were quite ancient, without admitting, however, that they were true fossils which had been deposited in remote periods.

The only other specimen seriously considered as a fossil is that described by Knowlton (1919), which was secured from a dealer in curios at Cuzco, Peru. Knowlton described this as being completely fossilized and expressed the opinion that it was at least several thousand years old. Although he conceded that it could not be adequately separated from certain living types, for example the *Copaca blanca* variety from the region of Lake Titicaca, he assigned to it the name *Zea antiqua*. Collins (1919a) in discussing Knowlton's fossil concluded that the origin of maize might now be transferred from prehistoric to geologic times. Later when he encountered an ear from a prehistoric grave near Arica, Chile, which resembled very closely the so-called *Zea antiqua*, he (Collins 1923) concluded that this was but added proof of the great permanence of the germplasm of maize.

This supposedly fossil ear has, on several additional occasions, been cited as evidence of the great antiquity of maize (cf. Kempton 1926, 1931, Collins 1931), and undoubtedly would have continued to be so cited by others had not dénouement come quite suddenly and unexpectedly when Brown (1934), suspecting that the specimen was not a real fossil, had it sectioned and showed conclusively that the object was an artifact, a very cleverly handmade replica of an ear of Peruvian maize, probably used as a rattle, for a cavity near the base contained three small, smooth, oval pellets.

So far as is known, there is extant today no fossilized maize, and after learning that the specimen which passed for fifteen years as a fossil finally proved to be a prehistoric rattle, paleobotanists will undoubtedly remain extremely skeptical of any future fossil remains of maize which may be discovered. We shall attempt to show later that maize as it is known today is probably a comparatively recent development, in terms of geological periods, in which case it is quite likely that time enough for fossilization has not been available.

Evidence from Archaeology and Ethnology

Archaeologists have had almost as great an interest in the problem of the origin of maize as have botanists, for it has long been evident that maize was the basic food plant of all ancient American civilizations and advanced cultures. Yet archaeological investigations have thrown but little direct light upon the problem of origin. They are of interest primarily in showing the great antiquity of maize as a cultivated crop in America and in establishing the fact that some of the types grown today were already in existence centuries ago. It is evident, in fact, from archaeological studies that whatever improvement has been made in the corn plant since its original domestication, has been achieved almost wholly by the Indians, and that the white man, until quite recently at least, has added but little to the heritage received from his aboriginal predecessors.

The Andean region of South America has been particularly fruitful in archaeological remains related to maize. The practice of burying the dead with various food products in a region where deterioration is extremely slow has resulted in a legacy to the present generation

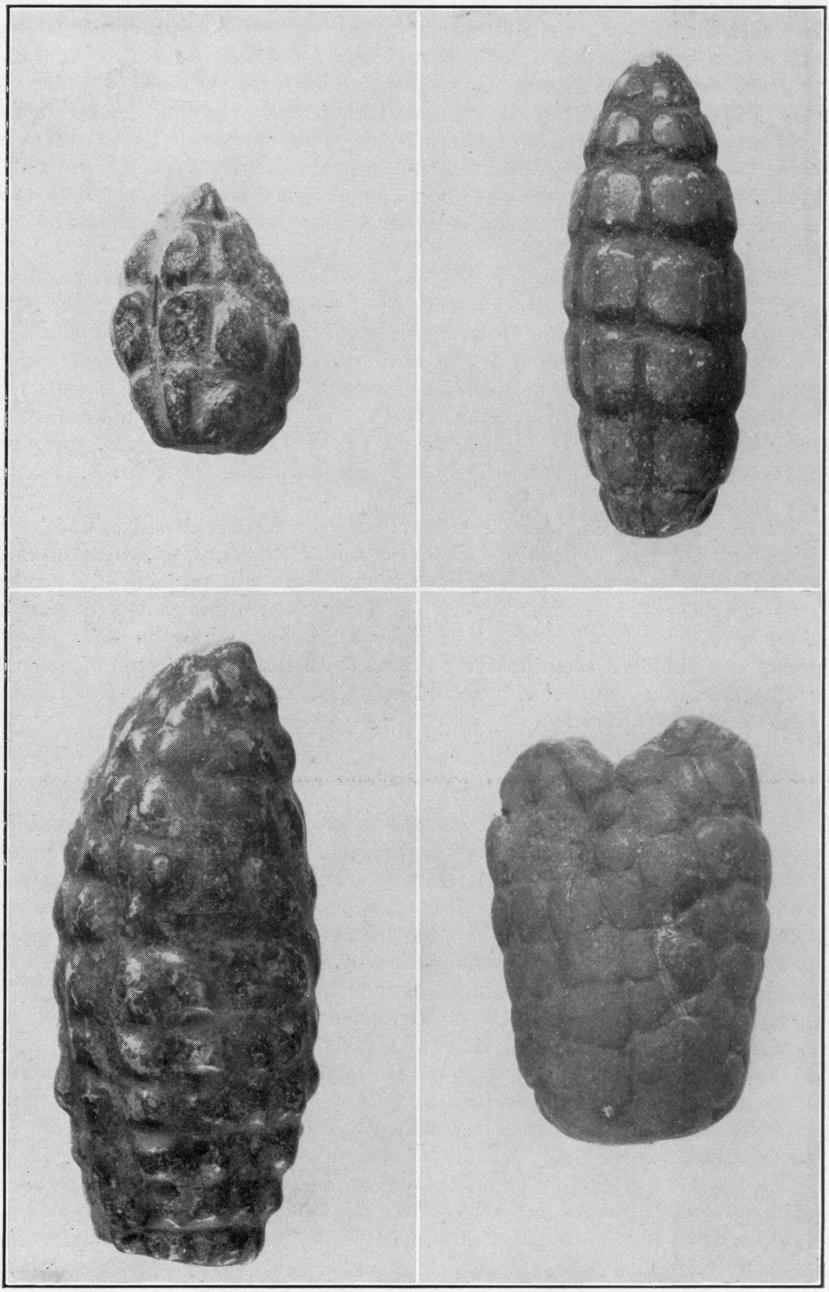

Fig. 14. Pre-historic carved stone objects from Peru. Several, perhaps all of these, are representations of maize ears. (Courtesy Field Museum of Natural History, Chicago, and American Museum of Natural History, N. Y.)

of a wide assortment of plant remains, including many ears of corn in an excellent state of preservation. Also, it was customary in the Andean region to represent various food plants in the pottery, and although many of the representations are highly conventionalized, others, particularly those of the Chimus on the Peruvian coast, are extremely realistic. Many of them were cast from molds formed from the original objects, so that they are, in reality, permanent replicas of prehistoric plant material. The common practice in the Andean region of burying in the land each season small fertility charms of clay or stone replicas of maize ears and other products has also left material evidence of the types of corn which were grown in the Andean region.

Some of the representations of maize found in the Peruvian pottery are illustrated in Figs. 14 to 17. Almost any of the types which are realistically represented could be duplicated in modern Peruvian varieties. Perhaps the chief points of interest in these prehistoric representations are that the small-seeded, pointed, pop corns of Mexico, the dent corns, and the giant-seeded soft corns of the Cuzco type are absent. Since the two first named types are almost completely lacking in Peru even today, we may conclude that they have been developed elsewhere. Since the large-seeded Cuzco type is quite common in Peru at the present time, we may conclude that this is a comparatively recent development. Tschudi (cf. Wittmack 1880) reported that he found two, now extinct, types of corn in pre-Incaic graves but he did not state how these differed from the modern varieties. Wittmack (1880) found one type with pointed seeds and very short thick ears having 12-22 rows, which he was not able to duplicate among modern varieties. He failed to find

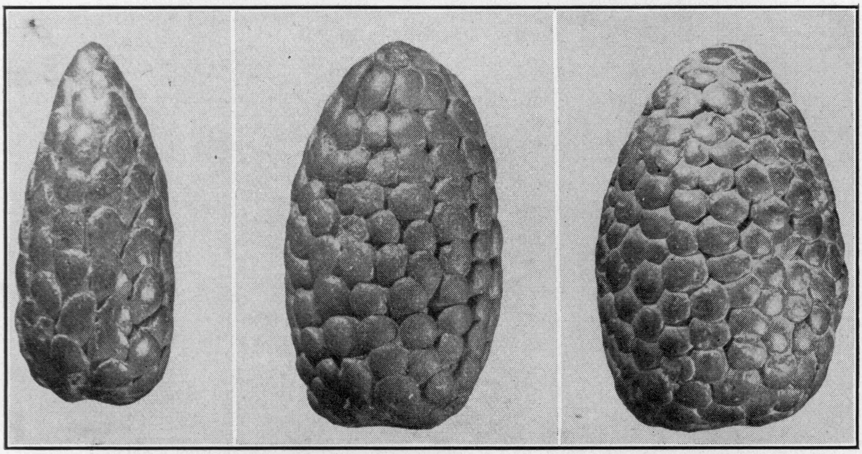

Fig. 15. Three pre-historic replicas of maize from Peruvian highlands. Natural size. Ear at left may represent pod corn. Compare with Fig. 92. (Courtesy Peabody Museum, Yale University.)

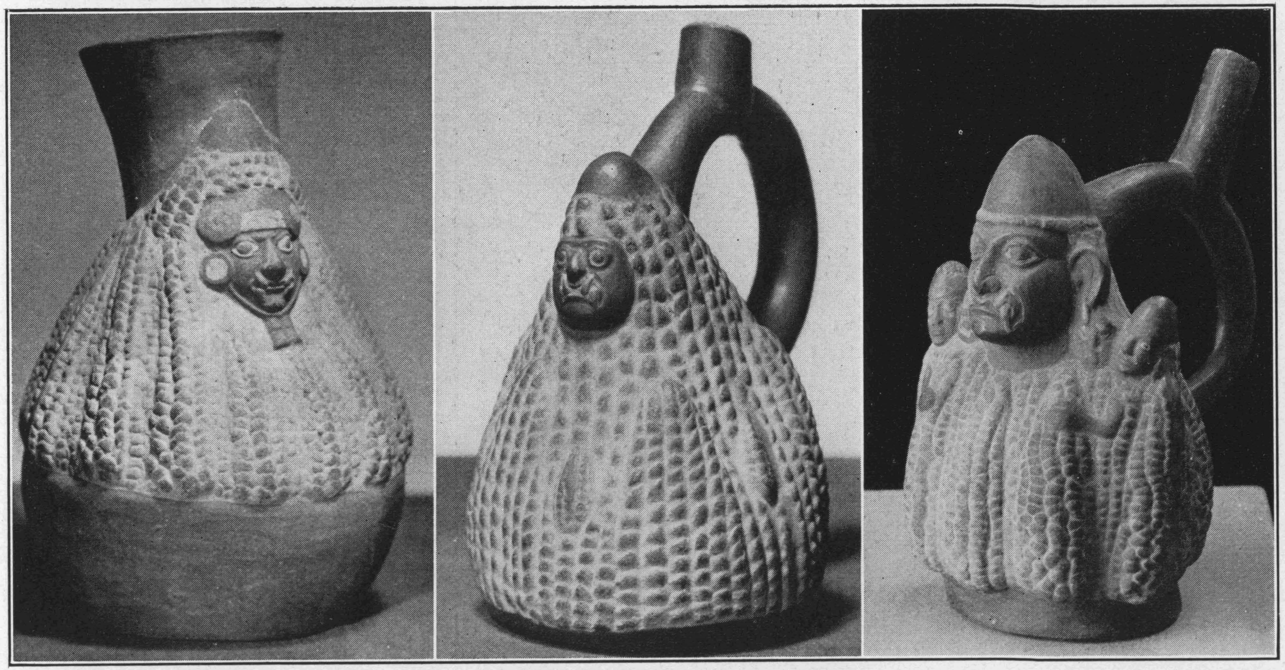

Fig. 16. Representations of maize on Early Chimu pottery of Peru. (Courtesy American Museum of Natural History, N. Y.)

either the Cuzco type or the North American dents or "Pferdezahnmaiz" among the remains collected at Ancon by Reiss and Stübel. Hendry (1930) has reported sweet corn among the prehistoric ears unearthed by Uhle at Huamachuco, Peru.

The archaeological evidence on maize from Central America and Mexico is even less illuminating. Representations of the maize-goddess are extremely numerous and testify to the superstitious reverence with which the plant was regarded by both the Mayas and Aztecs. But well preserved remains of prehistoric ears are almost completely lacking and realistic representations on the pottery are also extremely rare, though conventionalized figures are fairly common.

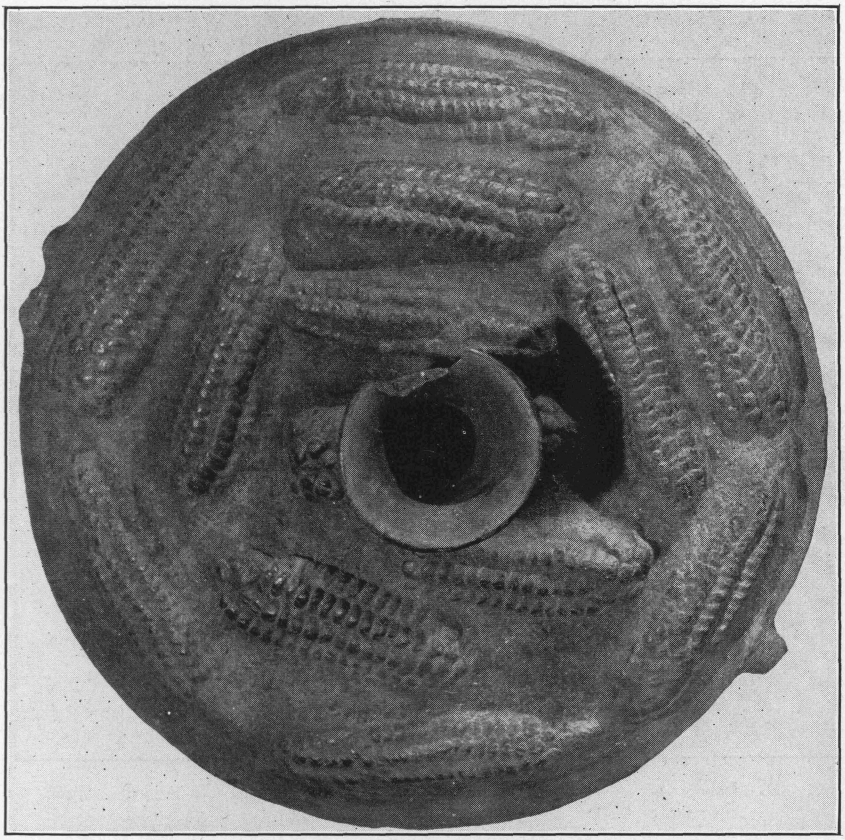

Fig. 17. Maize on Late Chimu vase from Peru. This is a comparatively recent prehistoric representation. (Courtesy Peabody Museum, Yale University.)

We are aware of only one good Maya representation, the little clay whistle illustrated by Maler (cf. Kempton 1926). In the Mexican pottery, however, are found a number of excellent representations of dent corn, one of which is illustrated in Fig. 18.

The corn of the southwestern Pueblo region falls into three distinct types associated with different culture periods. The period designated as Basket-Maker II is associated with the typical small-seeded, irregular-rowed tropical flint corns characteristic of Central America (cf. Kidder and Guernsey 1919). The period designated Pueblo I is associated with typical Mexican dent varieties, while the next stage, designated as Pueblo II, is associated with the long, slender, straight-rowed flint and flour corns which characterize the region today. The pointed pop corns are sometimes also found. Dent corn has also been found among the plant remains of the Bluff-Dwellers of the Ozarks, which incidentally is the only site where prehistoric seeds of Tripsacum have ever been collected (cf. Gilmore 1931). Among the remains of the Mound-Builders of the Mississippi Valley, particular attention is called to the observation by Wittmack (1880) of eight-rowed cobs in which the rows are distinctly separated in pairs.

Fig. 18. Dent corn on pre-historic Aztec vase. (Courtesy National Museum, Washington.)

The only additional evidence in this field which can be considered to

Fig. 19. Figure of the maize-goddess holding conventionalized ears of maize, Mexico. (Courtesy National Museum, Washington.)

have a bearing on the origin of maize is the fact that practically all Central American and North American tribes have legends of how maize first came to their people. Some of these traditions are fantastic in the extreme and merit little credence, but there is in almost all of them a conspicuous uniformity in one detail—that corn was not always known to them and came to them from elsewhere. The Peruvians are almost an exception in having no traditions or legends regarding the origin of corn (cf. Payne 1892).

Other significant facts which the archaeological evidence establishes are that the dent corns which were apparently absent in Peru in prehistoric times and which are still rare in that region were in existence in Mexico at an early date and also occurred in the Pueblo region of the Southwest as well as the Bluff-Dweller region of the Ozarks. On the other hand, the long, slender, straight-rowed types found in the Pueblo and Mound-Builder remains are absent in both Peru and Mexico. All of these facts have no immediate bearing upon the origin of maize, but they become explicable after the new cytogenetic data presented in this bulletin have been considered.

Evidence from Genetics and Cytology

Maize was the subject of study of some of the early plant hybridizers. It was, in fact, the occurrence of grains of several colors on the same ear due to segregation and the effects of foreign pollen which finally led to the correct interpretation of the mixing of varieties. From Tabernaemontanus, 1588, to Monti, 1719, at least twenty-two different individuals had recorded the occurrence of several types of grain upon a single ear. Camerarius, 1694, pollinated Ricinus with Zea pollen but it remained for Cotton Mather, 1716, to recognize and describe in detail, spontaneous crossing in maize. Thus maize was the first plant in which the results of hybridization were clearly recognized. Later observations of hybridization in maize were recorded by Dudley in 1721, Cooke in 1749, and Kalm in 1750.*

Since modern genetics does not date beyond the year 1900 and no cytological study conducted previous to that year contributed to our knowledge of the probable origin of maize, a history of the pertinent contributions of genetics and cytology might be expected to begin at the first of the twentieth century. Actually, however, the century was well along before any contributions were made by genetics or cytology.

The discovery of double fertilization in maize by Guignard (1901) contributed materially to our understanding of the pecular inheritance of endosperm characters that were under investigation even before the date of his publications, and De Vries, Correns, Webber, and numerous other early Mendelian geneticists used maize in their studies. But the work of these students contributed chiefly to the principles of heredity rather than to the origin of the plants under study.

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*Cf. Zirkle (1935) for detailed history of early experiments and obserations on hybridization of maize.

We may consider that the cytological work which had a bearing on the origin of maize had its inception in the work of Kuwada. Kuwada (1911, 1915, 1919, 1925) found that maize had various numbers of chromosomes, the variation, except in a few instances, being from 10 to 12 bivalents. His results were verified to a certain extent by later investigators, but for several years there was disagreement among the workers on some of the questions involved. Fisk (1925, 1927), Reeves (1925), and Randolph (1928a, b) agreed that the most common number was 10, and that in certain varieties a greater number often occurred. Kiesselbach and Petersen (1925) were unable to find any deviation from 10 bivalents after a study of 26 varieties, possibly for the reason that, by chance, they did not study any variety having a greater number of chromosomes. Longley (1924) first reported no departure from 10 chromosomes, but later (1925, 1927) he reported numbers in agreement with Kuwada, Fisk, Reeves, and Randolph. Longley (1924) further reported 20 bivalent chromosomes in *Euchlaena perennis* Hitchc., 10 in *E. mexicana* Schrad., and 10 in *Coix lachryma-jobi* L.

Randolph's (1928a) study of maize chromosomes was exceptionally complete, and he showed beyond doubt that in certain strains there are one to several chromosomes in addition to the 10 that are of regular occurrence. The 10 chromosomes always found he (1928b) designated as A-types, and the additional ones as B-types and C-types.

McClintock (1929a) reported a cytogenetic study of a triploid race of maize. She also (1929b, 1931a, b, 1932, 1933, 1934) described morphological characters of the chromosomes of maize by which the individual chromosomes can be identified. This work, though it has but little direct bearing on the problem of the origin of maize, established the basis for many of the cytogenetic investigations that followed.

Kuwada (1919) formulated a theory, as a result of his studies, that the variation in chromosome number in maize is the result of the plant's being of hybrid origin. In Florida teosinte, he found 10 pairs of chromosomes which were generally longer than those of maize. In hybrids between Florida teosinte and maize, he regularly counted 10 pairs, but two of the pairs were composed of members of different lengths. In his Figure 55, Pl. 2, the pairing in the bivalents, particularly in one of them, appears to be quite weak, and this may be significant in view of the results of later investigators. It should be stated, however, that Kuwada himself did not seem to attach much significance to the feebleness of pairing. He finally concluded that maize is a hybrid between teosinte and an unknown plant of the tribe Andropogoneae, thus agreeing with Collins as to its origin. In his earlier papers, he concluded that 12 (bivalents) was the original number in maize, but later (1925) he withdrew that conclusion and stated that he considered the original number to be 10. As far as we have been able to find, however, he did not modify his conclusion that maize originated as a hybrid between teosinte and some form of the tribe Andropogoneae.

Longley (1924) reported that in F_1 hybrids between maize and Chalco teosinte, 10 bivalent chromosomes of regular behavior occurred. This, in a general way, was a confirmation of the earlier results of a study of a similar hybrid by Kuwada (1919) already discussed.

Collins and Kempton (1914, 1916), in an attempt to hybridize Tripsacum x Euchlaena and Tripsacum x Zea, considered that they had effected patrogenesis when Euchlaena was used as the male parent and parthenogenesis when Zea was used. The former is the first recorded instance of true merogony. Their failure to obtain true hybrids between Tripsacum and its two nearest relatives appeared to most students to be a confirmation of the general opinion that Tripsacum was very distantly related to Zea and Euchlaena. It was only a few years later that Weatherwax (1923) reached the conclusion that Tripsacum should not be considered a member of the tribe Maydeae. Nearly two decades passed between the date of Collins and Kempton's first publication (1914) and that of any further published reports of attempts to hybridize Tripsacum with any of its relatives. However, considerable attention was given to hybrids between maize and Euchlaena.

Collins and Kempton (1920)* reported that in F_2 hybrids of maize and Euchlaena they found many instances in which characters from the different parents showed a tendency to combine more frequently than would be expected as the result of chance. No characters that they studied were found to be completely independent in inheritance and no strictly Mendelian inheritance was observed. Every character recorded showed significant correlation with one or more other characters, and these in turn were correlated with still others, with the result that all were interrelated and formed a single group. The nearest approach to Mendelian inheritance was shown by the arrangement of spikelets in the female infilorescence. Here the double spikelets were dominant in F_1, and the F_2 segregated in a ratio of approximately 3 to 1. It is of interest in connection with later discussion of the origin of Euchlaena (p. 189) that from a relatively small F_2 population, one plant identical with Euchlaena in its essential characteristics was obtained.

Langham (1938) has more recently verified the simple Mendelian inheritance of the difference between single and paired spikelets and has also shown that the two-ranked ear of Euchlaena and its strong response to length of day (cf. Emerson 1924, Kuleshov and Savran 1928) are inherited as simple genetic characters.

Kempton (1923) reported several different types of branching of maize ears, some of which were inherited as simple Mendelian characters and others apparently by no known Mendelian principle. Of particular interest in this study was one branched, eight-rowed ear which suggested its origin by the fusion of two four-row branches. Kempton (1924) continued this type of study by hybridizing Euchlaena with maize showing the crinkly, ramose, and brachytic characters. He concluded

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***Still earlier papers on hybrids of maize and Euchlaena, not directly cited here, are those of Harshberger, 1904; Vilmorin, 1907; Stok, 1910, and Lacy, 1913.**

that "the branching of the ramose variation, which would seem to represent a reversion to a more primitive form, does not approximate the branched inflorescence of Euchlaena, but is farther removed from Euchlaena than from normal maize." His results showed practically complete freedom of recombination of the characters that differentiate the two parents exclusive of the mutant characters. Kempton's data clearly indicate some linkage of the mutant genes with quantitative characters which differentiate the two genera (see p. 187).

The studies of Emerson and Beadle (1932) on crossing-over between Zea and Euchlaena chromosomes are outstanding in representing a new method of cytogenetic attack upon the species problem. They crossed different varieties of teosinte with stocks of maize in which all the maize chromosomes except number 8 were each marked by two genes. The F_1 hybrids were backcrossed with double-recessive maize stocks. Except in the *C-wx* region of chromosome 9 in hybrids of maize with Florida and Durango teosinte crossing-over occurred with approximately the same frequency as in Zea.* In hybrids of maize with Chalco teosinte and also with perennial teosinte, crossing-over occurred in the *C-wx* region; but in hybrids of maize with Florida and Durango teosinte little or none occurred in that region. Cytological studies by Beadle (1932a) showed that in the maize-Florida teosinte hybrid two pairs of chromosomes did not synapse normally. He found that in F_1 hybrids between Florida teosinte and maize, frequently one pair and less frequently two pairs were dissociated at diakinesis and metaphase of the first division. When one pair was dissociated the members were of different lengths; when two pairs were dissociated, there were two large and two small chromosomes. He also observed that the spindle attachments in chromosomes 2 and 3 of maize were in different positions from those of the homologous teosinte chromosomes. In F_1 hybrids of maize with Chalco and Durango teosinte, Beadle found no differences between the members of the bivalents; pairing was complete through metaphase and anaphase was regular. The reason for the much greater difference between the chromosomes of maize and Florida teosinte than between those of maize and Chalco or Durango was unknown, but Beadle gave credence to Collins' (1921) view that annual teosinte is a hybrid between perennial teosinte and maize. No rings or chains were found in the maize-Florida teosinte hybrids, as would be expected if translocations were assumed. Beadle also studied F_1 hybrids between Florida and Durango teosinte. He found greater irregularities in this hybrid than in any of the hybrids of teosinte with maize. This he interpreted as meaning that Durango and Florida teosinte resemble each other, cytologically, less than either of them resembles maize.

Beadle (1932b) made a special study of chromosome 9 in maize-

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*This is their conclusion. When all of the cross-over values, except those involving *C* and *wx* are averaged and compared with similar averages from pure corn, it is found that the average cross-over value in the hybrids is 23.3; in corn 28.5. There is also a significant deficiency of maize genes in several backcross populations, particularly that involving *su-Tu* and *d_1-cr*. These may be due to errors in classification but there is a possibility that other factors are also involved.

teosinte hybrids. Although little or no crossing-over occurred between the maize and teosinte chromosomes in the short arm, in the long arm it occurred with about the same frequency as in pure maize. For convenience in chromosome identification in his cytological studies, he introduced a reciprocal translocation involving chromosomes 8 and 9 so that cross-configurations at pachytene and rings of four chromosomes at post-diplotene might be observed if pairing was complete. A hybrid of normal and translocated corn was included in the study as a check. When all members of the quadrivalent came from maize, 96 per cent of the post-diplotene configurations were rings of four; when Durango teosinte was involved in the cross, 75 per cent were chains of four; and when Florida teosinte was involved, two pairs most frequently occurred, probably as the result of dissociation in two arms of the pachytene cross-configuration. At pachytene, a cross-configuration was the rule in all of the cultures, but this was because of non-homologous association which often occurs at that time. As a reason for this lack of crossing-over and the dissociation at post-diplotene, inversions in one parent, or general gene differences between the two parents in the non-homologous segments were suggested by Beadle.

Arnason (1936) made a cytogenetic study of hybrids of maize with Florida and Durango teosinte, similar to those previously conducted by Emerson and Beadle. His results were a general confirmation of those of Emerson and Beadle, except in a few details. He added that there was slight evidence of a structural difference between maize and Florida teosinte in chromosome 5, and that this may be one of the two unequal pairs; the other unequal pair is 8, 9, or 10; there is evidence that it is not 1, 2, 6, or 7. He reported that in maize-Durango teosinte hybrids, pairing seemed to be complete in chromosomes 1, 2, and 6. There was a suggestion that chiasmata are very rarely formed in relatively long segments of chromosomes 8 and 9.

Longley (1937) in a study of the comparative morphology and homologies of the chromosomes of maize, Euchlaena, and Tripsacum found the chromosomes of Euchlaena from southern Guatemala to be similar to those of Florida teosinte, and very different from those of maize. Euchlaena from northern Guatemala showed chromosome morphology indicating slight contamination with maize, and that from Mexico indicated still more contamination with maize. In general, the Euchlaena from southern Guatemala showed the fewest chromosome characters of maize, and the farther from that area the teosinte was native, the more maize characters the chromosomes exhibited. Collections made from Durango and Chapingo, Mexico, showed chromosomes scarcely distinguishable from those of maize. The terminal position of knobs on the chromosomes was regarded by Longley as a Euchlaena character, and it is of special interest that Tripsacum chromosomes were found to have only terminal knobs. Although terminal knobs are not uncommon on certain maize chromosomes, there is a possibility discussed later (p. 262) that they are derived from Euchlaena.

In Longley's studies, he used hybrids between Zea and Euchlaena in which the chromosomes of the two parents synapse, as material for comparative studies of chromosome morphology. In such hybrids, synapsis was usually complete, except that certain of the Euchlaena chromosomes were longer, and their ends extended beyond the ends of their Zea homologs. O'Mara (1938) has recently reported that the heteromorphic homologs found in Florida teosinte-maize hybrids and Durango teosinte-maize hybrids do not occur in hybrids between maize and the teosintes from Nobogame in Mexico or Nojoyá in Guatemala.

Cytogenetic studies of maize-perennial teosinte hybrids were reported by Longley (1924). During the first meiotic division in this hybrid he reported varying numbers of univalents, bivalents, and trivalents, with the univalents often lagging and failing to be included in the daughter nuclei. Pollen studies of the F_1 of perennial teosinte (homozygous non-waxy) x homozygous waxy maize showed 4 per cent waxy pollen. Longley interpreted this low percentage of waxy pollen as being the result of the loss of the univalent maize chromosome in a significant percentage of cases.

It is not necessary, however, to assume a loss of lagging univalent maize chromosomes; for if autosyndesis of the teosinte chromosomes were nearly complete, as appears to be the case (Longley 1934), the percentage of waxy pollen grains in the F_1 would be very small whether the lagging univalents were lost or retained.

Emerson (1929) reported genetic studies reflecting the behavior of chromosomes 4, 6, 9, and 10 in hybrids between maize and perennial teosinte, based on functional female gametes. His results indicate some intermediate condition between synapsis of all three homologs of each set followed by random disjunction and the synapsis of the two teosinte homologs, leaving the maize homolog unpaired. The maize chromosome of each set seemed to be distributed at random (to 50 per cent of the female gametes), but the teosinte chromosome was lacking in less than 16.7 per cent of the female gametes, showing that regular synapsis of all three homologs was to some extent displaced by pairing of only the teosinte homologs.

Longley (1934) reported that in F_2 and various back-crosses of the maize-perennial teosinte hybrid selective functioning of gametes occurred in favor of the parental gametic chromosome numbers. When plants with parental chromosome numbers were recovered they often had some characters inherited from the other parent; thus they must have obtained some genes from the parent having the different number, either by crossing-over or by the exchange of one or more chromosomes. Longley's cytological study of the F_1 hybrid showed that 10 bivalents and 10 univalents usually occurred, but occasionally two of the univalents paired weakly. The bivalents usually were from teosinte and the univalents from maize, but allosyndesis occurred as an exception. In backcrosses with maize, when the F_1 gamete had 20 chromosomes, there usually were 10 bivalents and 10 univalents at meiosis.

Fertile tetraploid hybrids between maize and perennial teosinte have been reported by Emerson and Beadle (1930), and again by Longley (1934) and Collins and Longley (1935). In neither case was the mechanism by which these plants occurred known, but they were definitely intermediate between the two parents and resembled maize-annual teosinte hybrids. They had 40 chromosomes in their somatic cells. Collins and Longley studied their tetraploid hybrid genetically to determine the relative amounts of auto- and allosyndesis. The waxy gene was involved in the cross and the expression of this gene in the pollen was used to determine the behavior of the chromosomes. Complete autosyndesis should give no waxy pollen, random pairing 16.7 per cent, and complete allosyndesis 25 per cent. In order to avoid skew distributions of percentages, Collins and Longley devised a formula for obtaining the coefficient of autosyndesis (t). By the use of this formula, when complete autosyndesis occurred, $t = 1$, with random pairing $t = 0$, and with complete allosyndesis $t = -1$. When this formula was applied in F_1 $t=0.80$, in F_2 $t=0.77$, and in F_3 t ranged from 0.54 to 0.82. These results indicate that the type of synapsis of these chromosomes is inclined to be autosyndetic, but that a significant amount of random pairing also occurs.

Attention should be called to the fact that in several of the investigations of pairing relationship between the chromosome of maize and perennial teosinte, chromosome 9 was assumed to be representative of the entire genom. While it is true that Emerson (1929), and Emerson and Beadle (1932) found no indication that chromosome 9 of perennial teosinte differs from any of the others so far as inheritance of marker genes is concerned, yet the studies of Emerson and Beadle (1932), Beadle (1932a, b), and Arnason (1936) show that chromosome 9 in Florida and Durango teosinte is lacking in homology with the corresponding maize chromosome. There remains some question, therefore, whether conclusions based upon this one chromosome are valid for the remaining nine.

Mangelsdorf and Reeves (1931) obtained true hybrids of Tripsacum with Zea and Euchlaena by the use of special techniques, and also (1935) a trigeneric hybrid involving all three genera. In the latter hybrid, pairing of the Zea and Euchlaena chromosomes was almost complete, with the Tripsacum chromosomes behaving as univalents. These results may be interpreted as meaning that Euchlaena is more closely related to Zea than to Tripsacum, which in turn is more closely related to both Euchlaena and Zea than had been thought previously. Although the difficulty of interpreting hybridization results in terms of taxonomic relationships is realized, there is now less reason than before for doubting that Zea, Euchlaena, and Tripsacum are members of the same tribe. (For a further discussion of details see p. 122.)

In order to determine whether the chromosomes of varieties of maize from greatly different geographical regions exhibited chromosome characters that would explain the diversity in the plants themselves, Cooper and Brink (1937) examined the chromosomes in hybrids of North American maize with about 68 varieties from Canada, Mexico, Central America, Bolivia, and Peru. Cytological results were those expected on the assumption that the diversity of forms of maize is the result of differences in genic constitution rather than chromosomal characters, except in two varieties. The origin of these two varieties was unknown, except that they came from South America. Various irregularities in chromosome behavior were observed in them, but because only a small portion of the varieties were irregular, the conclusion was drawn that there was little if any difference in chromosome structure within the genus Zea.

Powers and Clark (1937), and Powers and Dahl (1937) reported studies dealing with failure of pairing, which may have some bearing on the problem of the origin of maize. They tested goodness of fit between the variability and frequency distribution obtained from data on failure of pairing during diakinesis, and theoretical variabilities and frequency distributions based on hypotheses developed from theories regarding the phylogeny of the 10 pairs of chromosomes of *Zea mays*. Their results agreed best with the hypothesis that the 10 pairs of chromosomes respond as 7 independent units; that the first five units are composed of 2 chromosomes each, the sixth unit of 6 chromosomes, and the seventh unit of 4 chromosomes. On the assumption that distantly related chromosomes react as units to the forces causing failure of pairing, they regard this as further support of an assumption that maize is a secondary diploid having originated from a form with 7 pairs of chromosomes.

Longley (1938) studied chromosome morphology in maize stocks obtained from 33 tribes of Indians of the United States. His results showed few knobs on chromosomes of maize from northern Indians, slightly more on those of varieties from the Southeast, and many knobs on chromosomes of practically all maize from Arizona and New Mexico. The number of knobs increased as Mexico was approached, where the very knobby-chromosomed maize and maize relatives occur. Of all of the material studied, Longley did not find a stock of maize that was completely knobless. The nearest approach to this was in one variety of maize obtained from the Assiniboine Indians of Montana, in which 25 per cent of the plants had completely knobless chromosomes and 75 per cent had one knob on the short arm of chromosome 9. Of particular interest is the fact that Longley found in some of the Southwestern Indian corns unusual types of chromosome 10, that were very similar to types previously reported (Longley 1937) in Chapingo teosinte.

A brief summary of the bearing the cytogenetic studies reviewed in the preceding pages have upon the problem of the origin of maize must emphasize one fact above all others: the close relationship of Euchlaena to maize. Euchlaena has the same basic chromosome number as maize; it crosses readily with the latter to produce highly fertile hybrids in which chromosome pairing is almost complete and in which crossing-over between the chromosomes of the two genera is, with one exception, of the same order as that in pure maize. Some of the important characteristics by which Zea and Euchlaena are distinguished are inherited as simple Mendelian unit characters.

The situation in which two plants, classified by taxonomists as distinct genera, are hybridized as readily as Euchlaena and Zea and are so nearly identical in the architecture of their chromatin and germplasm is unique. This one fact, alone, raises the question whether the relationship of Euchlaena to Zea is not quite different from that which has been generally assumed.

Evidence from Morphology

Much of the work relative to the botanical origin of maize from the time of Ascherson to the present was based on the morphology of the ear. The ear is the most nearly unique organ of maize, since the entire plant is set apart from other grasses more by the characteristics of its ear than in any other way. Also, the characters of the ear by which maize differs from all other grasses are the very characters that disable the plant for survival in the wild state. If the manner by which maize acquired its ear from any related plant could be completely determined, the botanical origin of the species probably would not remain a difficult problem.

Ascherson (1880) stated that the first branched ear of maize to be mentioned in the literature was by a Sicilian, Paolo Boccone, whose observations were published in Robert Morrison's *Icones* in 1674. Naturally no evolutionary signficance would have been attached to such observations at such an early date.

Ascherson (1875, 1877, 1880) strongly emphasized the homology of the ears of maize and teosinte and described exceptional, outer, fruitless flowers in addition to the normal fruit-bearing flowers of the pistillate spikelets. He (1877) assumed that in wild corn the fruits were covered by husks, as in pod corn, but that pod corn itself could not have been the original, wild corn, because its husks are monstrosities and also because it reverts back to naked corn. He (1880) interpreted the maize ear as the result of fusion of lateral four-rowed spikes, the four rows consisting of two pairs of rows, with a terminal spike. Ascherson saw in teosinte the starting point for such a fusion phenomenon, and concluded that the fusion of the various spikes of a pistillate inflorescence of teosinte would be expected to result in a structure similar to the maize ear, and since in maize we sometimes find branched ears, the maize ear is the result of the fusion of the various spikes of the teosinte inflorescence and therefore maize is a descendant of teosinte. The branched ears of maize are thus regarded as reversions to the primitive form. Although Ascherson regarded these abnormal maize ears as branched, those that he considered to be most significant probably were branches of the culm bearing terminal ears and small accessory ears at nodes below the base. This view is borne out by the fact that he described one non-basal branch as being subtended by a shuck. This particular specimen fits Ascherson's hypothesis ideally, because teosinte inflorescences also show this special character. Ascherson reasoned, accordingly, that in the usual maize ear, the shucks subtending all except the basal spikes had disappeared and the spikes had subsequently fused.

Hackel (1887, 1890) separated Zea and Euchlaena on characters of the pistillate spikes. He stated that in Euchlaena the spikes of each leaf-axil are free and articulated, whereas in Zea they are grown together into a continuous, compound, and much-thickened axis. He stated too that the pistillate spike, perhaps originally through teratological development, corresponds to the cluster of spikes of Euchlaena, which have grown together to form a spongy, unbranched cob on which the indistinct double rows run lengthwise and are separated by shallow furrows. Hackel considered that pod corn may resemble the original corn in the development of its glumes, by the occasional division of the ear into more or less separate spikes, and by an indication of articulations in the inflorescence. But he thought the present condition of maize is perhaps an anomaly and is therefore scarcely typical. Harshberger's (1893) conception of the maize ear was practically the same as that of Hackel. He stated, "It seems that the fleshy cob has been formed by the union of several distinct spikes; this conclusion is strengthened on comparing Zea with Euchlaena or Tripsacum. A study of depauperate ears supports this view. A bifurcation of the tip frequently occurs, when the rachis is prolonged into two axes. The tissues sometimes separate sufficiently to show the different spikes which compose the fleshy cob." He stated further that each paired row of grains corresponds to a single spike of Euchlaena or Tripsacum.

Mrs. Kellerman (1895) conceived of primitive corn as having branches coming from several nodes, each branch being terminated by an inflorescence having both staminate and pistillate organs. Through natural selection the pistillate flowers became more abundant on the lateral branches of the plant and the staminate more abundant on the terminal, for plants having this tendency most completely expressed had an advantage. At the same time, the central spike of the lateral inflorescence, being in a more favorable position to obtain foods "drew into itself the main force of the branch and became more highly developed." She considered that the original corn had individual husks on the kernels like present-day pod corn, but with the shortening of the lateral branches the inflorescence became covered by subtending leaves and individual husks of the kernels were no longer produced.

Kellerman appears to have been the first writer who definitely pointed out the homology between the ear and the central spike of the tassel. Weatherwax (1935) cites Wigand (1854) as the first botanist to recognize the homology of the two structures. An examination of Wigand's publication, however, does not convince us that he understood in any way the homology between the staminate and pistillate inflorescence of maize; at any rate Wigand did not state clearly that he considered the inflorescences to be homologous, and his primary interest appears to have been in metamorphosis in a pre-Darwinian sense rather than in homologies or evolution. Goebel (1884) and Ascherson might also be considered as having regarded the ear and central spike of the tassel to be homologous, but if so, their conclusions are not clearly stated.

Schumann (1904) concluded that maize is a teratological variation of teosinte, fixed by culture. His conclusions, in general, were similar to those of Ascherson, and possibly were influenced by Ascherson, whose student he had been. However, Schumann did add the interesting hypothesis that the shucks of teosinte and maize are primitive organs, but that they are more highly developed than in primitive grasses and in that sense are specialized. He expressed the view that these modified leaves have entirely disappeared from the inflorescences of most grasses and from the staminate inflorescences of maize and teosinte, but that evidence of their past existence is shown only by the presence of callose collars.

Montgomery (1906) pictured the progenitor of maize and the phenomenon by which present-day maize came into existence in a rather different way. He suggested that the ear of corn developed from the central spike and that the ear of teosinte is a cluster of lateral branches. The occurrence of grains on the central spike of the tassel more frequently than on the lateral branches, in tassel-seeded strains, was used by Montgomery as the basis for his conclusion that the ear is the homolog of the central spike. He (1915) stated, however, "There is good evidence that corn was developed by evolution from teosinte or a near relative. . . ."

Wordsell (1916) concluded that "the structure of the maize-cob is the result of a phenomenon which would seem to be unique in the vegetable kingdom. It consists of the fusion of numerous spikes with flattened rachis, each bearing two rows of female spikelets, to form the thick female inflorescence usually termed the 'cob'." He explained the branched ear as the result of the "disruption" of the ordinary ear into its original component parts. Wordsell reproduced one of Ascherson's (1880) figures in connection with his interpretation; and although he stated that the spikes that fuse to produce the usual ear are two-rowed, the figure illustrating its disruption "into its original separate parts" shows several four-rowed lateral spikes disrupting from an eight-rowed central spike.

Collins (1912) pointed out that some varieties of pod corn have tassels with branches started in their reduction, and in such varieties there is little difference between the male and female inflorescences. He suggested that the maize ear may have developed from a branched inflorescence like the tassel, either by a complete loss of the lateral branches or by their reduction to the point where each branch is represented only by a pair of spikelets. He regarded pod corn as more primitive than common corn, and the latter more so than teosinte.

Collins later (1919c) proposed an entirely new theory to account for the polystichous structure of the maize ear. In hybrids of maize and teosinte a yoking of spikelets sometimes occurs. In some plants these yokes fit together at right angles to produce an eight-rowed ear. In others the ears are shortened and twisted in such a manner that a higher number of rows occurs. Collins thought that the polystichous structure of the ear of maize might have thus arisen through a yoking of alicoles accompanied by shortening and twisting of the inflorescence. Weatherwax (see p. 59) raised several pertinent objections to this theory.

Langham (1938) has recently revived, with modifications, Ascherson's (1880) theory that the ear of maize represents a fusion of the branches of the teosinte inflorescence. He states that the close relationship of the maize ear to the central spike of the tassel, and their origin by fusion of the two-ranked central branch of the teosinte tassel with one or more lateral branches are indicated by the following facts: (1) The number of pistillate spikelets on the ear varies directly as the number of staminate spikelets on the central branch of the tassel. (2) Maize with the two-ranked ear has the two-ranked central spike. (3) Partial fusion often occurs in F_2 populations of maize-teosinte crosses. (4) In segregating populations, the two-ranked ear is associated with the two-ranked central branch, and the many-ranked ear with the many-ranked central branch. This theory meets the same objection as other fusion theories; it leads to ears having rows of grain only in multiples of four. (See p. 59.)

Long before the end of the nineteenth century, many botanists realized that some of the peculiarities of the maize inflorescences were the results of the abortion of organs, and this realization played an important part in theories of the structural origin of the ear. Wigand (1854) described the abortion of the stamens in the fertile floret and the abortion of the other floret except its enclosing bracts. He presented a series of figures showing this and other phenomena. On account of the occurrence of stamens in early stages of development, Wigand stated that the pistillate florets of maize are perfect in earlier ontogenetic stages.

Goebel (1884) realized the abortive condition of pistils in the tassel and stamens in the ear of maize, for he stated that in both Zea and Coix the separation of the sexes has occurred from hermaphroditic flowers as a starting point. He stated further that each spikelet is two-flowered, one flower being terminal and the other lateral.

Hackel (1887), Harshberger (1893), and Baillon (1894) contributed evidence that the pistillate spikelet of maize bears a second, rudimentary flower, and Baillon also stated that the three stamens of the pistillate flower are reduced to staminodia. Poindexter (1903) contributed a publication on the development of the spikelet and grain of maize. He figured and mentioned briefly the rudimentary flower, but did not mention or show clearly the rudimentary stamens of the fruiting flower.

Schumann (1904) stated that the lower flower of the pistillate spikelet of maize does not develop, except the enclosing bracts; but that both flowers of the pistillate spikelet develop stamens to a feeble degree, and the primordium of a pistil occurs in the second flower. He stated that the two types of inflorescences have developed from a bisexual inflorescence by the abortion of pistils in the terminal and stamens in the lateral inflorescence.

Goebel (1910) derived the two inflorescences of maize as follows: In the ancestry of maize there was a grass which possessed distichously-branched terminal and lateral inflorescences with perfect flowers. With the thickening of the axis of the inflorescence polystichous branching occurred. The lower part of the inflorescence then became pistillate and the upper part staminate, by the abortion of organs of the opposite sex in each case. Following this a more marked spatial separation of the staminate and pistillate flowers occurred than in the rest of the Maydeae. In the lateral inflorescences the staminate terminal parts degenerated and in the terminal inflorescences the basal pistillate parts did likewise. The ear of maize probably arose by the suppression of its lateral branches in connection with the thickening of its main axis and its development by shucks. The lateral position of the ear is more favorable for the obtaining of foods than the terminal position of the tassel, and pistillate flowers develop only under more favorable conditions of food supply than is required for staminate flowers. This course of development of the ear made possible the production of a greater number of pistillate flowers and larger fruits than in the original inflorescence, and therefore is the principal surviving type.

Iltis (1911) considered the tribe Maydeae to be of polyphyletic origin, and that its genera descended from various groups of the Andropogoneae, some of which are now extinct. He considered Tripsacum to be most closely related to the Rotboellieae in the characters of its inflorescence and thickened glumes, but in Zea he saw affinities to the Ischaemeae, which consistently has two-flowered spikelets and a tendency towards the production of two kinds of flowers. In maize that was damaged by smut, Iltis observed numerous characters that he interpreted as showing affinities to the Ischaemeae and to some extent to the Rotboellieae also. Important among these characters were the tendency towards the production of perfect flowers, the production of two flowers in each spikelet (even the pistillate), the articulate rachis having concavities in which the fruits are sunken, and awns or awn-like structures. He also observed variations within the subtribe Ischaemeae, some of which were in the direction of present-day maize. Iltis agreed with Goebel (1910) in that he regarded the maize ear as homologous with the central axis of the tassel and that the lateral branches had been suppressed, for in his diseased plants he found tassels showing those tendencies. However, he considered that Goebel's hypothetical ancestor of maize, having a distichously-branched inflorescence, conformed to Tripsacum. Although Iltis' results were obtained mainly from parasitized plants, he thought the Andropogonaceous characters observed in maize to be merely "recessive abnormalities" or reversions to ancestral types. In this connection mention should be made of the observations of Weston and Craigie (1929) that the spikelets of teosinte, when malformed by Sclerospora, show a resemblance to pod corn in the overgrowth of the glumes.

The abortion of the lower pistillate flower, the existence of abortive stamens in the pistillate flowers, and abortive pistils in the staminate flowers of maize received special study by Weatherwax (1916, 1917), who showed the details of the phenomena. He demonstrated that abortion of stamens and pistils begins about the time of differentiation of spore mother cells, or before, thus showing that maize is morphologically perfect-flowered and has had a perfect-flowered ancestor. Stewart (1915) had shown that in Country Gentleman sweet corn both flowers of the spikelet usually develop either partially or completely, and Sturtevant (1899) and Kempton (1913) had mentioned other instances in which both flowers occasionally develop. Weatherwax interpreted these cases not as a primitive condition but as the development of the rudimentary ovary in the abortive lower flower. His reason for this interpretation was that the lodicules of this lower flower are the more developed of the two.

As to the structure of the ear in general, Weatherwax (1918, 1920) pointed out that in addition to the abortion of the lower flower and the stamens of the upper one, as in maize, both Euchlaena and Tripsacum have an entire pistillate spikelet of each pair in the aborted condition. With this knowledge at hand he criticised the fusion theory of the origin of the ear. This theory would mean, in the case of maize, the fusion of two or more spikes of four rows each. One member of each pair of rows of spikelets is abortive in Euchlaena but not in maize; thus the spike of teosinte has become two-rowed rather than four-rowed as its proposed homolog in maize would be. The fusion of two or more such hypothetical spikes of maize would therefore lead to ears always having multiples of four rows of grain, which is known to be contrary to fact. In commenting upon the theory that the ear is the homolog of the central spike of the tassel, Weatherwax pointed out that the theory contributes nothing towards explaining the polystichous character of the ear, the main problem to be solved, for the central spike of the tassel is itself polystichous. He (1923, 1935) considered that Collins' (1919) hypothesis of twisting and yoking falls short because the yoking of alicoles is highly improbable, and demonstrated that Collins was in error in his belief that when two rows of grains are dropped they are on opposite sides of the ear. He (1918) looked with more favor upon the hypothesis of Collins (1912) that the lateral branches are reduced to pairs of spikelets, because Gernert's (1912) ramose maize demonstrated the gradations in length of tassel branches by which the assumed reduction could have occurred. With the suggestions of Collins and Gernert as a starting point, Weatherwax developed a theory that seems to be in advance of any of those previously proposed. It will be considered in the next few paragraphs.

Weatherwax (1935) considers the ear to have developed phylogenetically from a panicle, by the reduction of its branches to such an extent that only a pair of spikelets represent each branch, this reduction already having occurred also in the central spike of the tassel.* He points out that in Setaria and Pennisetum, inflorescences occur that may be com-

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*Although Weatherwax does not mention unbranched tassels in connection with his theory of the origin of the ear, they are of frequent occurrence and seem to represent the ultimate stage in the phenomenon of reduction of branches which he emphasized.

pared to the ear of maize. Here the inflorescence is essentially a panicle, although its branches sometimes are so contracted that the whole structure resembles a spike, as the maize ear usually is considered to be. Among the species of Setaria, Pennisetum, and their relatives, and even in other tribes of grasses, it is easy to establish a series ranging from a typical panicle to a panicle so modified that it appears to be a typical spike. Botanists have shown no tendency to regard these inflorescences as any kind of monstrosities, because the explanation given above is sufficient.

Weatherwax explains the polystichous character of the ear on the basis of phyllotaxy. It is generally agreed that a branch of an inflorescence is homologous with and comparable to a branch of the vegetative stem. On vegetative stems branches ordinarily appear at the nodes, which are points of attachment of leaves; and in many branched inflorescences, modified leaves still occur at the points of origin of the branches. This gives a basis for the conclusion that leaves originally occurred at the points of origin of the branches on the inflorescences of grasses, including Zea; so that we may proceed to compare the arrangement of these branches with the arrangement of the leaves on the vegetative stem. Although all grasses ordinarily have the two-ranked arrangement of leaves, and the nearest relatives of maize also have this arrangement of their pistillate spikelets, the terminal inflorescence of maize and all inflorescences of many other grasses have a spiral arrangement of the primary branches of their panicles. In maize the pairs of pistillate spikelets and the alicoles also show a spiral arrangement on the cob; in fact the spikelets of Tripsacum and Euchlaena, the leaves of all grasses, and the pairs of staminate spikelets on the tassel branches of Zea itself may be considered as being in a simple spiral arrangement, for the distichous arrangement is only a simple form of spiral arrangement. There is fair agreement among botanists that the spike is more advanced than the branched inflorescence; that the spike has descended from the branched inflorescence by the contraction of the branches to such an extent that only a flower (spikelet in the grasses), or a cluster of them now represents each branch. In Setaria and Pennisetum, especially Pennisetum, the spike-like panicle may produce one or a few polystichous branches, apparently of the same nature that we sometimes find in a maize ear.

This theory of the nature of the maize ear requires that the arrangement of the primary branches of either inflorescence of maize be more complex than the arrangement of the leaves on the vegetative stem. It has already been stated that on both the stem and the main axis of the tassel a spiral arrangement prevails; but on the stem only one spiral occurs, whereas on the inflorescence several to many occur. This difference between the vegetative stem and the axis of the inflorescence is commonly observed in numerous other groups of plants as well as in the grasses themselves.

The ear of maize may be compared to the main axis of the tassel, because the two organs are homologous. One finds no difficulty in establishing a series of maize tassels showing a gradation in the length, abundance, and complexity of branches from the very elaborately branched to the unbranched form. The unbranched form is not uncommon, and is a structure that agrees closely with the maize ear and is homologous with it.

Supported by these facts, Weatherwax sees it necessary to postulate only that the numerous branches of the primitive paniculate ear are reduced to the point that they are represented only by pairs of spikelets; that such a contraction of branches has occurred in the panicles of numerous other lineages of plants has long been considered as established.

The morphological evidence of relationships among the genera of Maydeae also has been studied by Weatherwax. He (1918, 1935) showed the structure of the pistillate inflorescences and spikelets of Euchlaena and Tripsacum to be similar to each other and quite different from Zea in some respects. Tripsacum and Euchlaena are alike in having a brittle rachis with a developed and an abortive spikelet sunken into an alveolus in each internode, forming a distichous spike. The outer glume of the developed spikelet is indurated, and the spikelet includes two flowers the lower of which is abortive. Zea, on the other hand, differs strikingly from its relatives in that it has a polystichous ear and has both spikelets of a pair devoleped rather than one abortive.

In the staminate inflorescence, Weatherwax showed the structure of the spikelets to be similar in all three of the American genera, and, in fact, in all of the Maydeae. In his (1926) study of the Oriental Maydeae, he showed some similarities to the American group but also pointed out some differences that he considered significant. While the outer glume of the fertile pistillate spikelet is more or less indurated in all genera except Zea and Coix, the contents of this spikelet are protected by a combination of outer glume and rachis in Euchlaena and Tripsacum, and by the glume alone in Polytoca, Sclerachne and Chionachne. In Coix the grain is protected by a very hard spathe, and in Zea by shucks, the outer glumes in the latter having become reduced to inconspicuous scales.

The only additional morphological evidence that needs to be reviewed in connection with the present problem is that bearing on macrosporogenesis and related phenomena. Weatherwax (1919a) studied macrosporogenesis and embryo sac development in maize and showed that these phenomena are of the ordinary type; i.e., the micropylar macrospores of the linear group disintegrate, and an 8-celled embryo sac develops from the chalazal one. Cooper (1937) repeated this part of Weatherwax's study, and in addition made a similar study of annual teosinte and hybrids between teosinte and maize. Although Cooper's results on maize differed from those of Weatherwax in some minor details, the results of the two investigators were in general agreement. But more pertinent to the present subject is the fact that, except in a few very minute details, Cooper found teosinte, maize, and the hybrid to be alike, thus still more completely establishing the close relationship between maize and teosinte.

In summarizing the evidence from morphology it is obvious that on many points several interpretations are possible. On other points, however, the inferences are quite clear. There can be little doubt, for example, that the three American Maydeae—maize, Euchlaena, and Tripsacum—stem from a perfect-flowered ancestry. In all of them monoecism has occurred by an abortion of pistillate organs in the upper parts of the inflorescence or in the higher inflorescences and by an abortion of staminate parts in the lower. Moreover, there can be but little doubt that the ear is homologous with the central axis of the tassel, and that both have arisen through the loss of branches, probably by their reduction to spikelets; for any theory involving fusion of branches encounters the obstacle that it leads to ears in which the rows of grain occur only in multiples of four. Euchlaena is shown to be intermediate between Zea and Tripsacum in several morphological characteristics, resembling Zea more closely in some, Tripsacum in others.

PREVIOUS THEORIES ON THE ORIGIN OF MAIZE

We have, in previous sections, already discussed some of the theories dealing with the origin of maize, particularly those which are concerned with the morphological origin of the ear and other characteristics. We shall now consider the theories which deal more specifically with the botanical and geographical origin of maize.

Botanical Origin

There have been three general theories regarding the botanical origin of maize: (1) that it descended from pod corn, which differs from normal maize primarily by a single dominant gene governing the development of a brittle, readily disarticulating rachis and the production of prominent glumes enclosing the seed; (2) that maize originated from Euchlaena by direct selection, by mutations, or by the hybridization of Euchlaena with an unknown grass now extinct; (3) that maize, Euchlaena and Tripsacum have descended along independent lines directly from a remote common ancestor.

The first of these hypotheses apparently originated with Saint-Hilaire (1829), who having received from Brazil a fragment of an ear of pod corn, concluded that this was the natural condition of maize and that the glumes characteristic of pod corn were lost following cultivation.

Pod corn continued to be considered the primitive type by many botanists all of whom need not be mentioned here, as an extensive history of pod corn is presented later. Suffice it to say that almost all students of the problem of the origin of maize have been impressed by the primitive nature of pod corn, and even after dismissing it as the prototype of modern maize, for one reason or another, have frequently endowed the hypothetical ancestor of maize with many or all of the characteristics of this peculiar type.

De Candolle (1855), Darwin (1868), Körnicke and Werner (1885), Wittmack (1880), Ascherson (1877), and Hackel (1887) were of the opinion that pod corn could not be the primitive type either because it did not breed true or because it apparently sometimes arose spontaneously in cultures of normal maize. Sturtevant (1894) considered it the primitive type in spite of these facts, even though he verified them for himself. Collins (1912) recognized its primitive characteristics, regarded them as significant, and assumed that a pod corn-like form was one parent of the hypothetical hybrid from which maize had originated. In more recent years, however, the pod corn hypothesis has received but little serious consideration, especially since it has been demonstrated that pod corn differs from normal corn primarily by a single gene, that the pure or homozygous form of pod corn is usually sterile, and that numerous abnormalities almost as striking as pod corn, for example teopod maize (Lindstrom 1925), have appeared in the cultures of maize geneticists.

The theory that teosinte has played some rôle in the origin of maize may be said to have had its beginning with the work of Ascherson (1875, 1877, 1880), who showed convincingly for the first time that Euchlaena is the nearest known relative of maize. Ascherson (1880) considered the maize ear the result of a fusion of lateral spikes with a central spike, and he saw in teosinte the starting point for such a fusion phenomenon. He assumed that the fusion of various spikes of the pistillate inflorescence of teosinte would result in a structure similar to the maize ear, and since one of the chief differences between maize and teosinte is the profuse branching of the pistillate inflorescence of the latter and its absence in the former, he concluded that the maize ear was a fusion phenomenon and that maize is a descendant of teosinte.

Schumann (1904) concluded that maize is a teratological variation of teosinte, fixed by long cultivation. Like Ascherson he assumed that the maize ear represents the fusion of teosinte spikes.

The theory that teosinte was one of the parents of a hybrid from which maize had arisen had its origin indirectly in the so-called *Zea canina.* Harshberger, who had made a botanical study of this type and had concluded that it was the wild form, later discovered that it was nothing more than a natural hybrid of maize and teosinte (see p. 66). Thereupon he (1896) proposed two hypotheses of the hybrid origin of maize, (1) that it had originated from a cross of teosinte with an extinct closely-related grass, and (2) that maize is the product of a cross between wild teosinte and a cultivated race of teosinte developed, perhaps, under irrigation. Harshberger considered that a hybrid origin of maize would account for the many teratological variations and reversions which appeared under cultivation, and concluded that even if the view of a hybrid origin of maize were not accepted at least ". . . the fact that teosinte and maize can be crossed and a fertile progeny results shows that the two plants are united by the close and intimate bonds of kinship." Later

Harshberger (1911) described as the theoretical ancestor of corn a plant whose inflorescence would resemble in many respects that of Tripsacum.

Collins (1912) advanced the hypothesis that maize originated from a hybrid of teosinte and an unknown grass belonging to the Andropogoneae and similar to the earless or homozygous form of pod corn. He mentioned nine differences between pod corn and teosinte and showed that in most cases maize is intermediate. In later papers he (1918, 1919a, b, 1931) presented numerous reasons for considering maize as of hybrid origin. Its pronounced intolerance to inbreeding, and its marked heterozygosity are among the reasons emphasized most. The close resemblance between maize and the Andropogoneae and the frequent occurrence of Andropogonaceous characters in maize are the chief reasons for Collins' opinion that one of its parents must have been of the Tribe Andropogoneae.

In connection with the history of the hypothesis that teosinte played a rôle in the origin of maize, mention should be made of Blaringhem's (1907) highly original hypothesis that maize arose from teosinte as the result of mutations induced by injuries. Blaringhem was convinced that he had induced heritable variations in his cultures by injuring the plants and was of the opinion that maize arose from Euchlaena by this means. In this same connection we should also mention three alleged cases of the development under observation of maize from Euchlaena. The first is that of Burbank (1914) purporting to show that he had succeeded in obtaining maize from teosinte by eighteen generations of simple selection. The second is found in Blaringhem's (1924) report on photographic material received from Bento de Toledo in Brazil, illustrating the progressive change from teosinte to maize. It is obvious from the illustrations, as Weatherwax (1925) and Collins (1925) have already pointed out, that in both these cases selection started, not with pure teosinte, but with first generation hybrids of teosinte and maize. Selection did nothing more than recover maize-like ears from the segregating progeny, a commonplace occurrence in the cultures of geneticists. The third case was reported by Barusta (1938) who obtained tassel-seeded pod corn from plants that he believed to be teosinte, after crossing a form of "teocintli puro" having several-rowed ears with the typical form. From the tassel-seeded pod corn he then selected a naked-seeded type of maize. He advanced the interesting hypothesis that Tripsacum is the ancestor of the other two American genera of Maydeae, the sequence being: Tripsacum the parent of teosinte, teosinte the parent of tassel-seeded pod corn, and tassel-seeded pod corn the parent of normal corn. However, Barusta's figures and descriptions of his "teocintli puro" show convincingly that it was in reality a hybrid between teosinte and a very heterozygous form of maize, and that he merely repeated the error of Blaringhem and Burbank.

The third general hypothesis—that maize, Euchlaena, and Tripsacum are the products of independent and divergent lines of descent from a remote common ancestor (although it is implied by Harshberger 1896) apparently had its origin in Montgomery's (1906) suggestion that maize and teosinte are distinct coordinate genera developed from a common ancestor, now extinct, which he described as probably being ". . . a large, much-branched grass, each branch being terminated by a tassel-like structure bearing hermaphroditic flowers." East (1913) reached practically this same conclusion except that he regarded maize and teosinte not as distinct genera but simply as diverse types of the same polymorphic aggregation.

Although Montgomery himself later (1915) appears to have inclined toward the idea that maize originated from Euchlaena, Weatherwax (1918, 1919b) elaborated Montgomery's (1906) hypothesis to include Tripsacum as well as Zea and Euchlaena, all of which he assumed to have descended independently from a common ancestral form now extinct. He intimated that this hypothetical ancestral form was probably an Andropogonaceous plant and described it as "an herbaceous perennial, whose tall, jointed, leafy stems sprang from a rhizome. A branch was borne at practically every node of the aërial stem, each being somewhat shorter than the main stem and having about as many nodes as the latter above the point of branching. Branches upon branches occurred to the third and fourth or higher orders. The main stem and each branch was terminated by a loose, ovoid or pointed monopodially branched panicle. On this panicle the spikelets were probably borne in pairs, one sessile and one pedicelled, in many irregular peduncled clusters on the main axis and its branches. Each spikelet had two perfect flowers; the pistil had two feathery stigmas. From this plant the three genera here considered, and probably the other genera of the Maydeae and some of the Andropogoneae as well, have been evolved by the *suppression of parts*, whose rudiments are, in most instances, still to be found in the modern plants."

Weatherwax dismissed as unsatisfactory the other hypotheses which have been here discussed. He considered pod corn a reversion to a condition of the ear unprotected by husks and probably not a primitive form which has come down to us unchanged. The earless form of pod corn to which Collins attached considerable significance, Weatherwax considered to be the most highly specialized of all because of the occurrence of vestigial ear-buds in the axils of the leaves. Weatherwax regarded Harshberger's and Collins' theory that maize has had a hybrid origin (with teosinte as one of the putative parents) as unnecessary since the hybrid nature of maize had never been established. The marked intolerance of maize to inbreeding, which Collins considered evidence of its hybridity, Weatherwax explained as a possible result of limited opportunities for self-pollination under normal conditions.

On the other hand, Weatherwax's hypothesis of an independent origin of Zea, Tripsacum, and Euchlaena has been criticized on the grounds that the fundamental differences between Zea and other members of the Maydeae have been overlooked and that too much emphasis has been placed on the fact that the genera are alike in the suppression of sex organs (Kempton 1919). Collins (1931) admitted that Weatherwax's theory accounted for the fact that maize occupies a position intermediate between the Andropogoneae and other members of the Maydeae, but objected to it because of the long period of time supposedly required and its failure to take into account the close relationship of Zea and Euchlaena as indicated by their interfertility, their close agreement in number, size, shape and behavior of the chromosomes, and the fact that they are hosts to the same parasitic diseases.

It should be evident from this review that no completely satisfactory hypothesis of the origin of maize has, so far, been presented.

Wild Maize

In addition to the three general hypotheses on the origin of maize which are discussed in the preceding pages, some reference should be made here to the repeated reports and opinions that wild maize, essentially the same form as present-day cultivated maize, still exists or has existed until recent times.

Heller (1847) stated that in Mexico, single self-sown plants of maize flourish without culture, miles away from inhabited places, but he did not state that this was wild corn.

Sturtevant (1879) published a letter from Professor C. H. Brewer, who stated that in 1869 he had met a German botanist, Roezl, who informed him that he found in the State of Guerrero in Mexico an undescribed type of Zea which he considered specifically distinct, "the ears very small in two rows 'truly distichous'; the ear (but not each grain separately) covered with a husk, the grain precisely like some varieties of maize, only smaller and harder."

Watson (1891) received from Professor A. Dugés of Guanajuato, Mexico, under the designation "Maiis de Coyote" some specimens which answered Roezl's description. This corn was reported as growing wild at Moro Leon and the natives believed it to be the source of cultivated varieties. Watson described the plant as intermediate between maize and teosinte and designated it as a new species, *Zea canina.* He regarded the discovery of this form as the long sought solution of the problem of the origin of maize, stating that "we have here at last the original state of our cultivated maize." Bailey (1892) obtained seeds of this form from Watson and after a study of the plants grown from them as well as those resulting from their hybridization with cultivated maize he concluded that *Zea canina* was not a distinct species, although he agreed with Watson that it was the original form of common cultivated maize. Harshberger (1893) studied *Zea canina* botanically and published his results along with an extensive review of various other aspects which he thought pertinent to the problem of the origin of maize. He concluded that *Zea canina* was wild maize and that maize had originated in Central Mexico. Later, however, he was referred by Dugés to Professor Jose Segura of Mexico City, who wrote him that the "Maiz de Coyote" or *Zea canina* was nothing more than a hybrid of maize and Asesé (Euchlaena). A visit to Professor Segura in Mexico, who had been experimenting with artificial hybrids of maize and Euchlaena for five years, convinced Harshberger that this was true.

Nuttall (1929, 1930) found in the writings of Boturini, 1746, a reference to wild maize in Mexico, which she translated as follows:

"I found, in New Spain, a wild maize that grows amidst the forests or woods, especially those in the hot lands, with a small ear, whose few grains are of a more delicate flavour than the cultivated kind, as though Nature had located in them, as in a compendium, all of its essence."

Schellhas (1929) regarded this discovery as the solution of the problem of the origin of maize but Collins (1931) has raised several questions which cast serious doubt upon the accuracy of Boturini's statement. Nuttall (1930) is also responsible for an extract from a letter from Oliver La Farge, stating that in Guatemala there is a wild plant the small ears of which are used for food and have the unmistakable flavor of corn. Weatherwax (1935) and Kempton and Popenoe (1937) on separate expeditions to Guatemala in search of wild teosinte have investigated this report and the latter have succeeded in identifying the suspected young ears of maize as the inflorescences of an Aroid.

In spite of the disappointing, sometimes amusing, consequences which have followed the search for wild corn, we shall suggest later (p. 250) that there is a remote possibility that wild corn may still be discovered.

Geographical Origin

The question of the geographical origin of maize received attention much earlier than that of botanical origin. This is readily understandable; for the herbalists and earlier botanists, with rare exceptions such as Saint-Hilaire, had no conception of evolution and most of them held to the idea of the constancy of species and believed that each type represented an idea of the Creator. It had been assumed since ancient times that cultivated plants in general were merely wild plants that had been adopted by man. Consequently when maize was discovered the question of its origin was almost entirely one of geography, and the consideration of the problem of its phylogenetical or botanical origin has developed only within the past century.

Among the early botanists, there was considerable disagreement as to whether maize was of American or Eurasian origin, but this question has since been answered conclusively (see p. 34) and the only uncertainty that has remained is in regard to the particular region in America in which it had its origin. Saint-Hilaire, the first botanist to consider the botanical origin of maize, was also the first to suggest a definite geographical region, Paraguay, for its origin. De Candolle and Darwin both regarded the plant as South American and both assigned it to definite regions: Darwin to Peru and de Candolle to New Granada (now Colombia). De Candolle, however, admitted the possibility of a Mexican origin. Körnicke and Werner (1885) expressed the view that maize grew wild in the eastern, sparsely habitated part of Paraguay. Although the culture of the inhabitants of this region did not fit this assumption, they thought it probable that the original inhabitants might have sought homes elsewhere and then built up an advanced culture.

With the discovery of *Zea canina* (cf. Watson 1891, Bailey 1892, Harshberger 1893) and the later discovery that teosinte hybridizes readily with maize (cf. Harshberger 1896), the scene shifted from South America to Mexico. In spite of this fact, Sturtevant (1894) thought that the presence in Peru of the large-seeded Cuzco types, which he considered to be the product of a long period of domestication, pointed to a South American origin. He admitted, however, that the occurrence in *Zea canina* of pop corn-like grains, which he considered primitive, suggested Mexico as the place of origin.

Payne (1892), though not a botanist, evidently gave considerable thought to the origin of maize, and for this reason his conclusions may be of interest here.

"It is easy to understand how from Mexico the cultivation of maize may have spread to the valley of the Mississippi and to the Atlantic coast; and the fact that the agriculture of these districts was mainly concerned with the products of Mexican field-labor, maize, beans, and pumpkins, lends countenance to the view that the aboriginal agriculture of North America generally was in fact of Mexican origin. From Central America the cultivation of maize might similarly have been extended south of the Isthmus of Panama; but the fact that in South America we find a very large district in which maize agriculture was extensively practiced from remote antiquity, and from thence appears to have been carried eastward, westward, and northward, by tribes who were driven to migrate by the increase of population, renders it not improbable that the cultivation of maize had an independent origin in the Southern continent. This district is the basin of the Plate River and its tributaries. The Jesuit missionaries, following aboriginal tradition, always considered this to be the original seat of maize-agriculture, and the tunicated maize of Paraguay to be the original form of the corn. The Guaranis, as the maize-growing tribes of Paraguay were called by the Jesuits, were identical with the great maize-growing people calling themselves the Tupi, who migrated northward and eastward to the coast of Brazil; and there can be no doubt that the tribes who occupied the valleys which approached the plateau of Bolivia also originated in the Plate River Valley. From these last-named tribes the herdsmen of the Collao may have derived their first supplies of maize, the ear of which will not ripen in their own elevated district, and for the purpose of growing larger supplies they founded colonies in the valleys of the Cordillera to the westward on the Pacific coast. Ultimately they sent forth other offshoots in the valleys of the Andes to the eastward and northward. One of the last-mentioned colonies, founded in the valley of Cuzco, a district which produces the finest variety of maize yet known, became the centre of the dominion of the Incas. Though the question whether maize-agriculture did or did not independently originate in the South American continent is still doubtful, it is certain that Paraguay was a centre from which maize-growing tribes extended it in all directions, and highly probable that the maize-culture of the Inca dominion had Paraguay for its place of origin.

"It is consistent with this view that the traditions of the Incas, as far as they are known to us, give no account of the actual origin of maize-agriculture."

From 1896, the date of the appearance of Harshberger's paper, until within the past few years, the opinion has been almost unanimous that maize had its origin in Mexico. As Collins (1931) has stated, "The geographical region where maize was domesticated was one question about which there seemed no reason for controversy. Euchlaena, the wild plant most closely related to maize, is known only from Mexico. This evidence was considered conclusive and argument was confined to the rival claims of particular Mexican localities."

After Vavilov (1926, 1927) had developed the hypothesis that the center of formation of any cultivated species is frequently the region showing the greatest number of distinct cultivated or wild types, Collins (1931) noted that if this criterion were applied to maize the center of distribution would be northwestern South America and not Mexico. Vavilov himself (1931a), however, reached a different conclusion and assigned its origin to the Central American-Mexican region, largely, however, because teosinte was native there.

Kempton and Popenoe (1937) discovered teosinte growing as the dominant species over thousands of acres in western Guatemala near the village of San Antonio Huixta. They concluded from this discovery, that if teosinte is involved in the origin of maize, the most probable region of origin is in the Maya highlands of western Guatemala, rather than in Mexico.

It is evident in reviewing the history of theories on the geographical origin of maize that the close relationship of maize and Euchlaena has been the most important factor in assuming a Mexican origin. The earlier botanical students were almost unanimous in their opinion that maize had originated in South America. After *Zea canina* was discovered and the hybridization of maize and Euchlaena demonstrated, the argument for a Mexican origin seemed so conclusive that archaeologists permitted it to color their opinions on the origin of the pre-Columbian American cultures and civilizations (cf. Spinden 1917, Nuttall 1926, Morley 1931). More recently, as it has become more and more evident that it is extremely difficult to show how Euchlaena, in spite of its close relationship to maize, has had any part in its origin, a note of doubt about the Mexican-Central American origin of maize has appeared. Weatherwax (1938), for example, who had previously (1923) considered radical the assumption of a duplicate origin, has finally concluded that maize may have had two centers of origin, one in Central America, the other in Peru.

We shall present later, new cytogenetic evidence which indicates that

Euchlaena has played no part in the origin of maize and that there is no longer any necessity of seeking the primary center of origin of maize in Mexico or Central America.

NEW EVIDENCE FROM CYTOGENETIC STUDIES

Many competent studies on the cytogenetics of Zea, its closest relative Euchlaena, and hybrids between them, have already been made, but most of these have had for their objectives the solution of fundamental problems in genetics and cytology and these particular genera have been used primarily because they provided favorable material. Our objective has been a slightly different one, for we have been concerned primarily with the problem of the origin of maize. Consequently we have concentrated our efforts, so far as possible, on filling in the gaps in the available knowledge bearing on the problem. This has, in some cases, resulted in the pursuit of routine studies, which were in themselves of minor importance but which we believed to have a bearing on the general problem. In the discussion which follows we have combined the results and observations of other writers with our own, making no distinction between the two, except, of course, to cite the literature upon which we have drawn so freely.

Chromosome Numbers and Behavior in Maize and Relatives

Zea mays L.: That the normal chromosome number of maize is 10 has been so well established by numerous studies already reported that it needs no further discussion here.

Euchlaena mexicana Schrad.: The chromosome number of *Euchlaena mexicana* was reported by Kuwada (1919) as $n = 10$, $2n = 20$. Since Kuwada's report appeared, these numbers have been amply verified by many investigators. Although it was done incidentally to other cytological studies, these numbers have been verified many times during the present study. Randolph (unpublished) reported B-type chromosomes in *E. mexicana* very similar to those of maize. Longley (1937) confirmed Randolph's findings.

E. perennis Hitchc. has 20 bivalent chromosomes in its pollen mother cells, this number being just twice that occurring in *E. mexicana* and showing that the species is tetraploid. This number was first reported by Longley (1924).

Tripsacum dactyloides (L.) L. **diploid:** Three varieties of *Tripsacum dactyloides* have been found to have 36 chromosomes in their root tips. These were obtained from Atchison, Kansas; Manhattan, Kansas; and Angleton, Texas. Although cytological studies were made on all three forms, results of the studies of meiotic phenomena will be given only for the one from Angleton, Texas, as it is believed to be a good representative of the group.

No exceptions were found to 36 as the number of chromosomes in the root tips (Fig. 20A). At diakinesis, pairing of chromosomes is regular and there are 18 pairs (Fig. 20B). The pairs vary considerably in size, some of them being approximately the size of Zea chromosomes. The usual size, however, is smaller. After diakinesis the chromosomes line up on the equatorial plane in a fairly regular fashion and the two members of each pair separate. At the time of disjunction a small amount of lagging is sometimes observed (Fig. 20C), but the usual behavior is that all of the chromosomes go approximately together to the poles and are included in the daughter nuclei. The chromosomes undergo something of a reorganization during interphase, as the individual chromosomes appear to lose their identity and coalesce. They line up at the second division metaphase and pass regularly to the poles (Fig. 20D). The final result is that a regular bilateral quartet of microspores is formed.

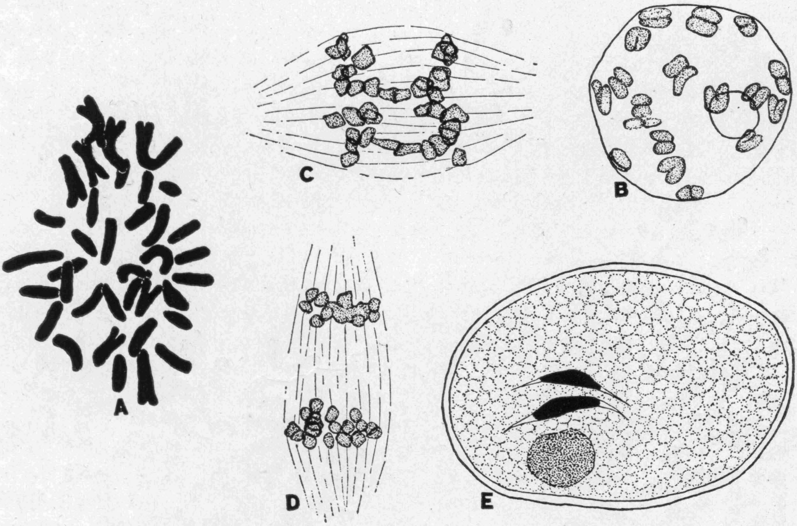

Fig. 20. *Tripsacum dactyloides* (2n), the form obtained from Angleton, Texas. A. The 36 chromosomes of a cell from a root tip; X 2550. B. Nucleus of a pollen mother cell showing 18 bivalent chromosomes of approximately regular behavior; X 2025. C. Anaphase of division-I, showing slightly late disjunction in two bivalents; otherwise the behavior is regular; X 2025. D. Regular anaphase of division-II; X 2025. E. Mature pollen; X 1035.

The pollen grains are uniform in size and have one germ pore. The division of the generative nucleus to form two crescent-shaped male nuclei occurs before the pollen tube is formed (Fig. 20E). The tube nucleus is approximately spherical. Our observations on the structure of the pollen of Tripsacum are in close agreement with Weatherwax's (1923) previous studies of the pollen of Zea.

T. dactyloides (L.) L. (tetraploid), usually having 72 chromosomes in its root tips, has been obtained from several sources. The forms obtained from the different localities show obvious differences in external characters of the plants, but they are almost identical cytologically. The variety studied most closely was collected near New Haven, Connecticut. In this form pairing at diakinesis is not nearly so regular as in the forms having 36 somatic chromosomes. Very seldom can 36 bivalents be counted and some of the bodies are multivalent (Fig. 21A). The number of multivalent chromosomes varies from cell to cell but seldom or never do all the chromosomes of a cell unite in pairs. At diakinesis they may be either quadrivalent, trivalent, bivalent, or univalent. These chromosomes line up on the equatorial plane on a fairly uniform row, disjoin, and pass to the poles; but some irregularities are seen here (Fig. 21B), such as lagging and fragmentation. The number of chromosomes passing to

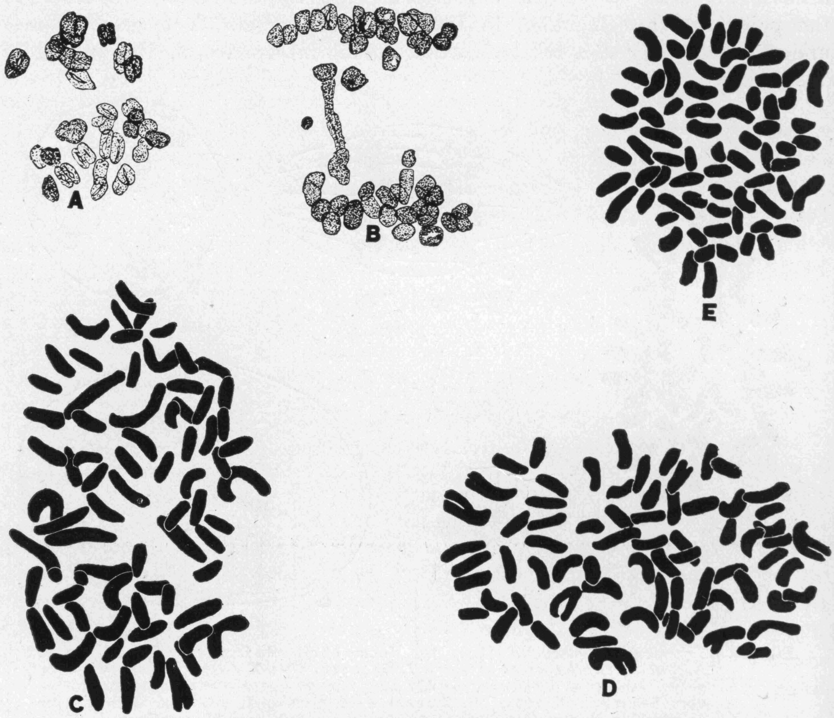

Fig. 21. Chromosomes of *Tripsacum dactyloides* (4n). A.-C. The form obtained from New Haven, Connecticut. A. Diakinesis showing multivalent and bivalent chromosomes in the same cell; X 1325. B. Anaphase of division-I; lagging and a fragment; X 1325. C. The chromosomes of a root-tip cell; X 2550. D. The form obtained from Miami, Florida; 72 chromosomes of the root tip; X 2500. E. The form obtained from Nacogdoches, Texas; 72 chromosomes of the root tip; X 2500.

each pole is often difficult to determine, probably because a variable number of them are bivalent or trivalent. The behavior of the chromosomes during telophase and interphase does not differ significantly from that of diploid *T. dactyloides*. Metaphase and later stages of the second division are usually, although not always, regular and this is also true of the bilateral quartet and the pollen grains.

An unusual amount of variation and irregularity may be expected to occur in polyploid plants in which the chromosomes combine in numbers greater than two. Therefore it is not surprising that the tetraploid forms of *T. dactyloides* are quite variable in vegetative characters. There are many forms of them and the forms occurring in different localities are seldom alike. It is probable that a considerable portion of the gametes produced by these plants are non-functional because they have received an irregular number of chromosomes. The number of chromosomes may vary slightly among the individual plants. The number 72 is most frequent and no variation has been observed in the root tips (Fig. 21C) during this study, but all of the material examined probably came originally from only a few plants and represents only a small number of samples. Longley (1924) reported 35 as the reduced chromosome number in *T. dactyloides*. However, the fact that closely related forms have 18 as their reduced number, combined with our observations of 72 in the root tips, points to the conclusion that 36 rather than 35 should be considered as the typical reduced number in this group.

Other forms of *T. dactyloides* having 72 as their unreduced number of chromosomes and about 72, totaling the components of the univalents, bivalents, trivalents, and quadrivalents, in their pollen mother cells were obtained from near Miami, Florida (Fig. 21D) and Nacogdoches, Texas (Fig. 21E). Other material, showing about 72 as the total number of chromosomes in the pollen mother cells, but of which counts in root tips were not made, was collected at Alpine, Texas; San Antonio, Texas; and Jackson, Mississippi.

It is probable that the forms of *T. dactyloides* having 72 chromosomes as their prevailing number are autotetraploids of comparatively recent origin.

T. latifolium Hitchc. Chromosome counts in the root tips of *T. latifolium* usually showed 72 chromosomes (Fig. 22A) but the number seems to vary slightly. In the pollen mother cells the number is difficult to determine on account of the presence of multivalent chromosomes. The chromosomes unite in a great variety of ways. Univalents, bivalents, trivalents, quadrivalents, and probably higher combinations may be observed in the same cell (Fig. 22B).

At metaphase of the first division the chromosomes line up irregularly (Fig. 22C) and pass to the poles. Many irregular conditions were found also at the end of the first and second divisions.

On the whole this species is more irregular than the tetraploid forms of *T. dactyloides*. Some plants, however, are not extremely irregular and produce good pollen. Longley (1924) has described meiosis in *T. latifolium,* pointing out its irregularities and stating that the reduced chromosome number is about 35. As the number probably varies, plants may be found having as few as 70 chromosomes in the unreduced condition. However, counts made from the pollen mother cells of this species should not be considered as reliable as those made from root tips because there is no massing of chromosomes in the root tips as there usually is in the pollen mother cells, so that counting in the root tips is less difficult even though the number is greater.

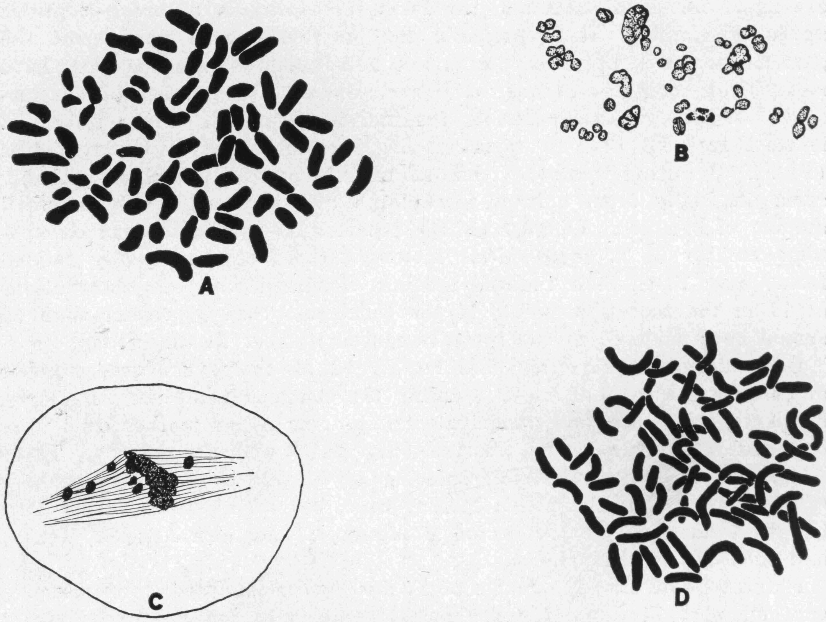

Fig. 22. A-C. Chromosomes of *Tripsacum latifolium.* A. The 72 chromosomes of the root tip; X 2550. B. Pollen mother cell showing univalents, bivalents, and higher combinations of chromosomes; X 1175. C. Metaphase of division-I, showing lagging of several chromosomes; X 865. D. *T. laxum;* the 72 chromosomes of the root tip; X 2000.

Tripsacum laxum Nash usually showed 72 chromosomes in its root tips (Fig. 22D). Occasionally the number seemed to be 70, 71, or 73; but the number 72 was most common.

Coix spp. The chromosomes have been counted in the root tips of four species and varieties of Coix, all of which were obtained from Professor Paul Weatherwax.

C. aquatica Roxb. has 10 chromosomes as the unreduced number (Fig. 23A). This is believed to be the smallest number of chromosomes reported in the Gramineae, the only other member of the family having this number being *Sorghum versicolor* Anderss. (cf. Longley 1932, Karper and Chisholm 1936). The somatic chromosomes of *C. aquatica* often show prominent constrictions. No variation in the number was found.

C. lachryma-jobi L. and varieties *stenocarpa* Oliver and *ma-yuen* Stapf have 20 chromosomes as the unreduced number (Figs. 23B, C, D). *C. lachryma-jobi* (Fig. 23D) appears to have shorter and thicker chromosomes than the other 20-chromosome forms, but this may be a result of differences in fixation.

Sclerachne punctata R. Br. Chromosome counts were made from the root tips. In the material studied the unreduced number was consistently 20 (Fig. 23E). The chromosomes are rod-shaped, vary somewhat in size, and bear a general resemblance to those of many other species of the Maydeae.

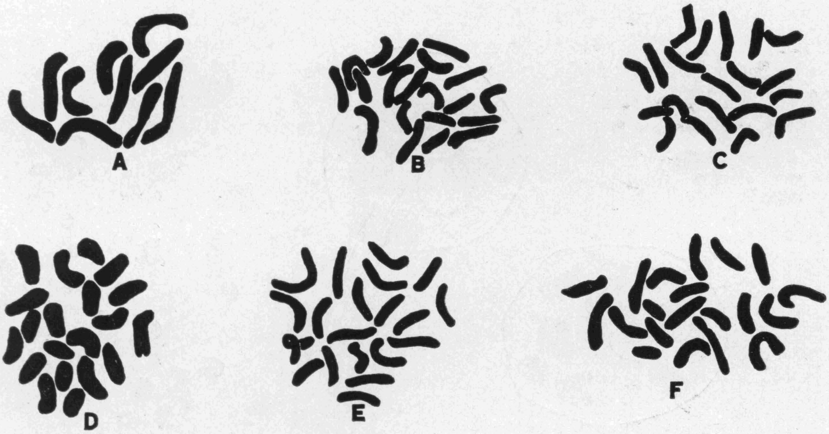

Fig. 23. Chromosomes of root tips of Oriental species of Maydeae; X 2550. A. *Coix aquatica*, 10 chromosomes. B. *Coix lachryma - jobi* var. *stenocarpa*, 20 chromosomes. C. *Coix lachryma - jobi* var. *ma-yuen*, 20 chromosomes. D. *Coix lachryma - jobi*, 20 chromosomes. E. *Schlerachne punctata*, 20 chromosomes. F. *Polytoca barbata*, 20 chromosomes.

Polytoca barbata Stapf. Counts of chromosomes in the root tips consistently showed 20 chromosomes (Fig. 23F). The chromosomes were not found to be distinguishable from those of *Sclerachne punctata*.

Manisuris cylindrica (Michx.) Kuntze. Although manisuris is not now classified in the tribe Maydeae, it was formerly considered a species of Tripsacum. This coupled with Weatherwax's (1926) observation that Tripsacum shows a closer morphological relationship to Manisuris than to the other genera of the Maydeae has led us to include *Manisuris cylindrica* in this study. The material from which this study was made was collected in Bryan, Texas. Root tips proved to have 18 chromosomes

(Fig. 24A) and pollen mother cells nine bivalents (Fig. 24B). One pollen mother cell was found to contain 10 bodies at diakinesis (Fig. 24C), but two of these probably were univalents. Members of the pairs are loosely attached at this time and may easily separate.

The critical stages of meiosis were studied and found to be regular. Although the chromosomes are paired loosely during early diakinesis (Fig. 24C), they appear to be united very closely in late diakinesis (Fig. 24B). During the first division, metaphase is regular but the chromosomes cannot be counted from lateral view. The anaphase also is regular. At telophase the univalent chromosomes coalesce at the poles which are quite near the cell wall. The second division also is normal and a regular bilateral quartet results. The quartet is formed by two successive, centrifugal, cytoplasmic divisions, as in *Zea mays*.

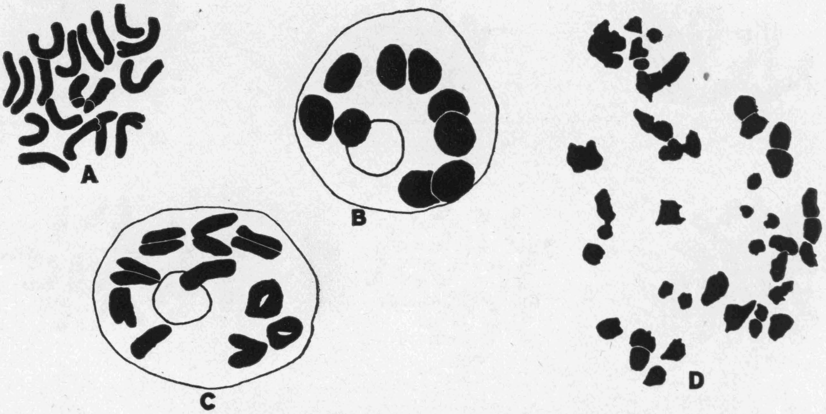

Fig. 24. A-C. Chromosomes of *Manisuris cylindrica*; X 2550. A. The 18 chromosomes of a root-tip cell. B. Pollen mother cell at diakinesis, showing 9 bivalent chromosomes closely paired. C. Pollen mother cell, showing 8 bivalent chromosomes loosely paired and the separated members of another bivalent; slightly earlier than B. D. Chromosomes of *Tripsacum dactyloides* (4n) X *T. latifolium* (4n) at late prophase of division-I; X 1300.

Although the haploid number of chromosomes in *M. cylindrica* is only nine, no attempt was made to identify the various individual chromosomes. They are of approximately the size of those of the Tripsacums and usually appear rather uniform in size and shape.

That Manisuris has a haploid chromosome number of nine is a noteworthy fact. This number suggests a relationship of Manisuris and Tripsacum, since in Tripsacum the reduced numbers known at present are 18 and 36. The addition of Manisuris to the series gives us 9, 18, and 36, whereas in the other Maydeae and Andropogoneae the most common reduced numbers appear to be 5, 10, and 20.

Manisuris cylindrica is recorded by Hitchcock (1935) as occurring quite generally over the Southeastern United States. It is assigned by him, and most other systematic botanists of recent years, to the tribe Andropogoneae.

The resemblance of Manisuris and Tripsacum has long been recognized; in fact, *M. cylindrica* was assigned to the genus Tripsacum and called *Tripsacum cylindricum* by Michaux in 1803 (cf. Hitchcock 1935). The old literature shows many other instances of the assignment of Manisuris and Tripsacum to the same tribe. The most striking differences between the two genera are that Manisuris has perfect flowers and Tripsacum does not and that Tripsacum has the staminate and pistillate spikelets in separate portions of the inflorescence; and these differences may not be sufficient justification for considering the relationship of the two genera to be very remote.

Avdulov (1931) reported *Rottboellia glandulosa* Trin., a close relative of *M. cylindrica*, as having 54 (a multiple of 9) chromosomes in its somatic cells. He suggested, however, that *Tripsacum dactyloides* may have 80 somatic chromosomes rather than 70 or 72 and that its basic number is therefore probably 10. Also he did not consider *T. dactyloides* as being closely related to the other Maydeae, not being aware that it had been hybridized with Zea and Euchlaena. Hunter (1934), as a result of a cytotaxonomic study, concluded that both Tripsacum and Coix occupy isolated positions in the tribe.

A summary of the chromosome numbers of Zea and its relatives determined by our studies is given in Table 1. (Cf. also Reeves and Mangelsdorf 1935.)

Table 1. Summary of chromosome counts in relatives of maize

	n	2 n
Euchlaena mexicana Schrad	10	20
Euchlaena perennis Hitchc	20	40
Tripsacum dactyloides (L.) L.		
Collected at Angleton, Texas	18	36
Collected at Manhattan, Kansas	18	36
Collected at Atchison, Kansas	18	
*Collected at Nacogdoches, Texas	36	
*Collected at San Antonio, Texas	36	72
*Collected at New Haven, Connecticut	36	72
*Collected at Miami, Florida	36	72
*Collected at Jackson, Mississippi	36	
**Trispsacum laxum* Nash	..	72
**Tripsacum latifolium* Hitchc	36	72
+**Tripsacum pilosum* Scribn. and Merr	..	72
Coix lachryma-jobi var. *stenocarpa* Oliver	..	20
Coix lachryma-jobi var. *ma-yuen* Stapf	..	20
Coix lachryma-jobi L.	..	20
Coix aquatica Roxb	..	10
Sclerachne punctata Brown	..	20
Polytoca barbata Stapf	..	20
Manisuris cylindrica (Michx.) Kuntze	9	18

*These forms are regarded as autotetraploids. Some multivalent chromosomes are formed by them during meiosis, and this probably results in slight variations in chromosome numbers.

+On two occasions plants have been received under the name *T. pilosum*, and in both cases the plants showed 72 chromosomes in their root tips. However, there is some question whether these plants were actually *T. pilosum*.

Crossing Relationships

At the time that these studies were started, only two true intergeneric or interspecific hybrids among the Maydeae had been recorded: *Zea* *mays* x *Euchlaena mexicana* and *Zea mays* x *E. perennis*. Crosses of Tripsacum with Zea and Euchlaena had been attempted by Collins and Kempton (1914, 1916) but these yielded only matroclinous and patroclinous plants. We discovered early in our investigations that the pollen grains of Tripsacum germinated on the styles of Zea, that the pollen tubes entered the styles, and that fertilization was readily accomplished if the styles of maize were cut back to a length approximately that of Tripsacum styles. Following this discovery we attempted a number of hybridizations which previously had appeared to offer no promise of success, including in these attempts a number of genera which are not classified as members of the tribe Maydeae.

Crossing Techniques

In every case where pollen from a short-styled species such as Tripsacum was applied to long-styled species such as Zea or Euchlaena, the styles of the latter were cut back to a length approximately that of the short-styled parent. This technique has already been described in a previous paper (Mangelsdorf and Reeves 1931) and need be mentioned but briefly.

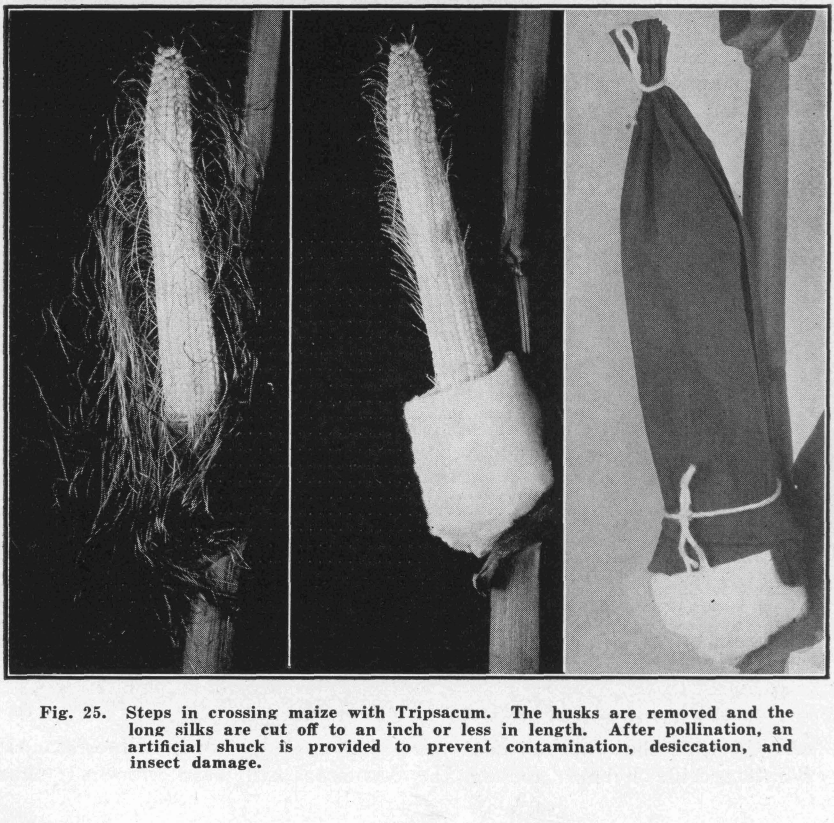

Fig. 25. Steps in crossing maize with Tripsacum. The husks are removed and the long silks are cut off to an inch or less in length. After pollination, an artificial shuck is provided to prevent contamination, desiccation, and insect damage.

here. In the case of corn the entire shuck is removed by a circumcision at the base of the ear. The silks, which are receptive almost their entire length, are cut back with a pair of shears. After pollen has been applied, the ear is covered with an artificial shuck consisting of a piece of crepe paper wrapped around a strip of cotton felt which has been wound around the base of the ear. The resiliency of the cotton and the flexibility of the crepe paper allow for the growth of the ear, usually without any further adjustment. The steps involved in this technique are illustrated in Fig. 25.

It might appear that cutting back of the styles would be unnecessary so long as the bases of the styles are exposed to pollination; but, whether because there is a greater wastage of pollen when the entire length of the silks is exposed, or whether the pruning operation has an actual beneficial effect, the fact remains that hybrid seeds are set in greater abundance when the silks are excised.

In crosses on teosinte the silks are pruned in the same way, but no artificial shuck is provided as any seeds which may develop are naturally protected by a hard shell.

Most of the crosses attempted on the various species of Tripsacum were made early in the season before any Tripsacum pollen had been shed. In some cases, however, crosses were made on inflorescences which had been bagged before the styles had appeared, and from which the staminate portion of the inflorescence had been removed.

Observations on Pollen Tube Growth and Nucellar Stimulation

In the majority of crosses which were attempted, microscopic examination of the styles was made within twenty-four hours after pollination to determine whether the foreign pollen had germinated and if the pollen tubes had entered the styles. In some of the later experiments, however, the sudden wilting of the styles soon after the application of pollen was considered adequate evidence that the pollen tubes had entered.

As crosses of Zea and Tripsacum frequently result in parthenocarpic ovules in which there has been a marked stimulation of the nucellus but in which endosperm or embryo tissue is not found, the swelling of the nucellus may be regarded as an indication of a successful pollination, even though fertilization has not been accomplished or the fertilized egg has not divided.

Results of Crosses

Zea x Euchlaena mexicana. This cross is readily effected when either genus is used as the pistillate parent and in fact it occurs quite frequently in nature in regions where the two genera occupy the same habitat. When maize serves as the pistillate parent, the seeds are frequently partially aborted and some are germless. There is no difficulty, however, in obtaining living hybrid plants from either cross. The hybrids are highly fertile, the degree of fertility varying with the variety of teosinte used as the parent. In some crosses the F_1 plants exhibit variability in the pollen and many empty grains are in evidence (Fig. 72). The cytology of this hybrid has been studied by Kuwada (1919), Longley (1924), Beadle 1932a, b), Arnason (1936), and the genetics by Collins and Kempton (1920), Kempton (1924a), Emerson and Beadle (1932), and Langham (1938). Earlier studies on *Zea canina,* which was later shown to be a natural hybrid of Zea and Euchlaena, have already been discussed in a previous section of this paper, and additional genetic studies by the present writers are reported later (p. 172). We have encountered one instance of maternal endosperm in this cross (p. 85).

Zea x E. perennis. Like the preceding cross, this one is easily effected using either genus as the pistillate parent. When maize serves as the pistillate parent, however, the seeds are usually decidedly aborted and in some cases all the seeds on a crossed ear are germless. The hybrid is partially fertile but exhibits a high percentage of empty pollen (Fig. 72). Genetic and cytological studies have been made by Longley (1924, 1934), Emerson (1929), Emerson and Beadle (1930, 1932), and Collins and Longley (1935). We have done very little work with this cross because we have suspected *E. perennis* of being a recent autotetraploid having no immediate bearing on the problem of the origin of maize.

Zea x Tripsacum dactyloides (4n). When maize with shortened styles is crossed by tetraploid *T. dactyloides,* seeds are set on almost every ear, the percentage of seeds set sometimes approaching 100. The seeds are small, usually fairly well developed, but frequently germless. Maternal endosperm is sometimes encountered and one case is discussed later (p. 84). Maternal embryos have never been definitely identified.

The reciprocal cross often produces some shrivelled, aborted seeds, none of which have ever been successfully grown. Whether these are true hybrids or parthenogenetic diploids has not been determined.

When the shell of Tripsacum contains no seed it remains dull and pithy. When it contains a normal seed it becomes glossy and horny. When it contains a shrivelled seed resulting from pollination with maize, it is intermediate, exhibiting sufficient glossiness and horniness to distinguish it from empty shells; but these characteristics are by no means as well developed as in normal seeds.

Zea x Tripsacum dactyloides (2n). We have made this cross on a more extensive scale than any other, and since the results from this cross have led to new hypotheses regarding the origin of corn, they are discussed in considerable detail in a later section (p. 94). Suffice it to say here that though the cross is difficult to make, hybrid seeds can be produced in large numbers by the use of the technique already described. Few of the hybrid seeds, however, reach maturity; and those which do can be germinated only under optimum conditions. From crosses in which approximately 185,000 silks of maize were exposed to pollen of this form of Tripsacum, we finally obtained 29 living hybrid plants.

From the reciprocal cross Tripsacum x Zea we have never obtained viable seeds. Shrivelled, abortive seeds are sometimes produced, accompanied by a partial hardening of the shell which encloses the seed. But seeds well enough developed to be capable of germination have not occurred. It is, of course, much more difficult to make pollinations on Tripsacum in large numbers than on maize, for a single pollination on an ear of the latter involves several hundred ovules while a similar pollination on Tripsacum involves only ten to twenty.

Zea x Tripsacum latifolium (4n). When Zea is used as the pistillate parent, some hybrid seeds are always produced. None of these so far obtained have been viable but if pollinations were made on an extensive scale, there is little doubt that living hybrid plants could be obtained. The reciprocal cross has never, in our experiments, produced any seeds.

Zea x Coix spp. Crosses of maize by *Coix aquatica* and *Coix lachryma-jobi* have produced neither seeds nor nucellar stimulation although in the case of the latter the pollen tubes have been observed to enter the styles. Reciprocal crosses have not been attempted.

Euchlaena mexicana x E. perennis. This cross is readily effected using either species as the pistillate parent.

E. mexicana x Tripsacum spp. Euchlaena pollinated by either the diploid or tetraploid form of *T. dactyloides* has borne a few seeds, none of which have been viable. In the cross of Euchlaena x diploid Tripsacum, chromosome counts in cells of the embryo and endosperm were made. The numbers found, 28 and 38 respectively (Figs. 26A, B), indicate that the seeds were true hybrids.

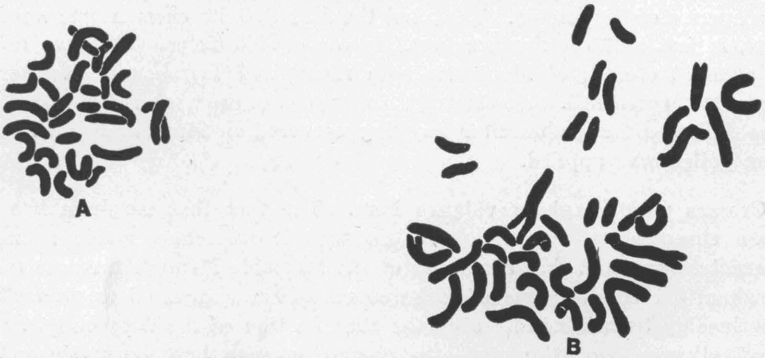

Fig. 26. Chromosomes of *Euchlaena mexicana* X *Tripsacum dactyloides* (2n); X 2550. A. Cell of the embryo; 28 chromosomes. B. Endospern cell; 38 chromosomes (in 2 drawings).

Seeds have also been produced when the reciprocal cross was made but these, too, were not viable. No seeds have been obtained in crosses with *T. latifolium* in which the latter served as the pistillate parent. No observations on nucellar stimulation have been made in this cross.

There is little doubt that living plants of the hybrid Euchlaena x Tripsacum could be produced if crossing were attempted on a large scale. The F_1 hybrid of Zea x Tripsacum crosses as readily with Euchlaena as with either parent and Euchlaena is closer, morphologically, to Tripsacum than is Zea.

E. perennis x Tripsacum spp. We have pollinated perennial teosinte by various kinds of Tripsacum again and again during the past nine years and have never obtained a single seed in hundreds of pollinations. It is rather difficult to understand why these pollinations should be so completely fruitless, for similar ones made upon annual teosinte usually result in the production of abortive seeds.

The cross of *E. perennis* with tetraploid Tripsacum would be an extremely interesting one, for it would probably result in a true-breeding amphidiploid. But until an improved technique is developed it appears to be impossible to make this cross.

Tripsacum spp. inter se. All of the species or forms of Tripsacum in our collection hybridize readily with each other. The tetraploid *T. dactyloides* crosses easily with the diploid. Either form of *T. dactyloides* produces seed when pollinated with *T. latifolium.* The reciprocal crosses have not succeeded, perhaps because the number of attempts was small. *T. laxum* in our cultures has never flowered, so that no crosses with this species have been attempted.

Crosses with Manisuris cylindrica. As previously mentioned, Manisuris is usually classified in the Andropogoneae, but earlier botanists considered it a species of Tripsacum. This, and the fact that its chromosome number, nine, is just half the number found in the diploid Tripsacum, have led us to attempt crosses of Manisuris with maize and Tripsacum. Neither of these has succeeded. An attempt to cross Sorghum and Manisuris has also failed, although nucellar swelling occurred in Manisuris when sorghum pollen was applied.

Crosses with Sorghum vulgare Pers. The fact that sorghum has the same chromosome number as maize, that it resembles maize in many characteristics, and that a number of the heritable Mendelian recessives of sorghum are counterparts of those of maize has suggested to us a closer relationship than is admitted by the classification of the taxonomists. Accordingly we have attempted a number of crosses, both on maize and on sorghum. The latter have been greatly facilitated by the use of the method of bulk emasculation by treatment with hot water (Stevens and Quinby 1933) and by the male sterile types reported by Karper and Stephens (1936) and Stephens (1937). In spite of the use of methods which have permitted pollinations to be made on a large scale, no seeds have been obtained in the cross of sorghum x maize or its reciprocal. In the latter, however, there has sometimes occurred the same type of nucellar swelling which occurs so frequently when Tripsacum pollen is applied. Sorghum is the only plant tested except Euchlaena and Tripsacum, whose pollen stimulates nucellar swelling in maize. We suspect that the development of improved pollinating techniques may eventually result in hybridization of maize and sorghum. Such hybrids have on several occasions been reported but all claims which have been thoroughly investigated have proved to be without foundation.

Summary of Crosses

The results of these numerous crossing attempts are summarized briefly in Table 2. Unless otherwise noted the number of pollinations made has been large, usually including hundreds and sometimes thousands. This is particularly true of most of the crosses which have not succeeded, for most of these were attempted again and again over a period of years. We are, therefore, reasonably certain that the crosses which failed in our experiments will continue to fail until improved techniques are developed.

Parthenogenesis in Intergeneric Crosses

Collins and Kempton (1914, 1916) reported a cross of Tripsacum x Euchlaena which resulted in a single patroclinous plant exactly resembling the pollen parent, Euchlaena, and breeding true for this condition for three generations. Another cross, that of Tripsacum x Zea gave rise to several plants which were completely maternal, exactly resembling Tripsacum in their characteristics. These crosses are of interest from several standpoints. The former represents the first published example of merogony in plants and one of the few examples of this phenomenon on record (cf. East 1934). Both cases represent instances of induced parthenogenesis in genera related to maize, one quite closely related. They suggest the possibility of inducing parthenogenesis in maize as well, and the further possibility of utilizing this phenomenon in developing homozygous strains of maize, thus accomplishing in a single step a result that now requires five, six, or more generations of inbreeding. East (1930) has already discussed the possibilities of crop improvement through this method.

Because of these practical considerations, we have maintained throughout these crossing experiments a constant search for instances of induced parthenogenesis. In our earlier experiments none were encountered, and in a previous paper (Mangelsdorf and Reeves 1931) we were inclined to question the results reported by Collins and Kempton. Later experiments, however, have shown that parthenogenetic development, at least of the endosperm, may sometimes occur.

Table 2. Summary of results obtained from attempted interspecific and intergeneric crosses in the Maydeae and Andropogoneae

Pistillate parent	Staminate parent	Pollen tubes entered styles	Nucellus swelled	Hybrid	
				Seeds produced	Plants obtained
1. Zea mays	Euchlaena mexicana	x	x	x	x
2. Zea mays	Euchlaena perennis	x	x	x	x
3. Zea mays	Tripsacum dactyloides 4n*	x	x	x	x
4. Zea mays	Tripsacum dactyloides 2n*	x	x	x	x
5. Zea mays	Tripsacum latifolium 4n*	x	x	x	–
6. Zea mays	Coix lachryma-jobi*	x	o	o	o
7. Zea mays	Coix aquatica*	–	–	o	o
8. Zea mays	Sorghum vulgare*	x	x	o	o
9. Euchlaena mexicana	Zea mays	x	x	x	x
10. Euchlaena mexicana	Euchlaena perennis	x	x	x	–
11. Euchlaena mexicana	Tripsacum dactyloides 4n*	x	x	x	o
12. Euchlaena mexicana	Tripsacum dactyloides 2n*	x	x	x	o
13. Euchlaena mexicana	Tripsacum latifolium 4n*	x	–	–	o
14. Euchlaena mexicana	Sorghum vulgare*	x	–	o	o
15. Euchlaena perennis	Zea mays	x	x	x	x
16. Euchlaena perennis	Euchlaena mexicana	x	x	x	–
17. Euchlaena perennis	Tripsacum dactyloides 4n*	x	–	o	o
18. Euchlaena perennis	Tripsacum dactyloides 2n*	x	–	o	o
19. Euchlaena perennis	Tripsacum latifolium 4n*	x	–	o	o
20. Tripsacum dactyloides 4n	Zea mays	x	x	x†	o
21. Tripsacum dactyloides 4n	Euchlaena mexicana	x	–	x†	o
22. Tripsacum dactyloides 4n	Tripsacum dactyloides 2n	x	x	x	x
23. Tripsacum dactyloides 4n	Tripsacum latifolium 4n	x	x	x	x
24. Tripsacum dactyloides 4n	Manisuris cylindrica	x	–	o	o
25. Tripsacum dactyloides 4n	Sorghum vulgare	x	–	x†	o
26. Tripsacum dactyloides 2n	Zea mays	x	x	x	o
27. Tripsacum dactyloides 2n	Euchlaena mexicana	x	x	x	o
28. Tripsacum dactyloides 2n	Tripsacum dactyloides 4n	x	x	x	x
29. Tripsacum dactyloides 2n	Tripsacum latifolium 4n	x	x	x	x
30. Tripsacum dactyloides 2n	Sorghum vulgare	x	–	o	o
31. Tripsacum dactyloides 2n	Manisuris cylindrica	x	–	o	o
32. Tripsacum latifolium 4n	Zea mays	x	–	o	o
33. Tripsacum latifolium 4n	Euchlaena mexicana	x	–	o	o
34. Tripsacum latifolium 4n	Tripsacum dactyloides 4n	x	–	o‡	o
35. Tripsacum latifolium 4n	Tripsacum dactyloides 2n	x	–	o‡	o
36. Sorghum vulgare	Zea mays	–	–	o	o
37. Sorghum vulgare	Tripsacum dactyloides 2n	–	–	o	o
38. Sorghum vulgare	Manisuris cylindrica	x	–	o	o
39. Manisuris cylindrica	Zea mays	x	–	o	o
40. Manisuris cylindrica	Tripsacum dactyloides 4n	x	–	o	o
41. Manisuris cylindrica	Sorghum vulgare	x	x	o	o

*Styles of pistillate parent cut back before pollination.
x—indicates success; o—failure; –, no observations.
†Aborted seeds obtained. Not known whether these are hybrids or haploids.
‡Only a small number of pollinations made. Since the reciprocal of this cross is easily effected, it seems probable that this one would succeed if enough pollinations were made.

Maternal Endosperm in Crosses with Tripsacum

In 1931 a maize stock homozygous for waxy endosperm was crossed with the tetraploid *T. dactyloides* from Connecticut. Three ears were obtained, all of which bore some seeds with waxy endosperm. Since the endosperm of Tripsacum is always non-waxy and as these seeds were obviously not normal corn seeds resulting from accidental self-pollination, it appeared that we were dealing with a case of parthenogenetically induced endosperm development. These same ears also bore many germless seeds and it occurred to us that parthenogenetically induced embryos may also have arisen, but that these, being haploids, had not survived*

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*Viable haploid plants of maize have been discovered by several investigators but the possibility still remains that the majority of haploid embryos do not survive.

while the maternal endosperm, which was presumably diploid, had succeeded in maturing. There was no marked relationship between maternal endosperm and germlessness among the seeds, the ratio being as follows: normal non-waxy, 53; germless non-waxy, 179; normal waxy, 18; germless waxy, 30. All of the waxy seeds containing embryos were planted and all which grew produced typical hybrid plants differing in no essential way from the hybrids arising from non-waxy seeds.

More recently we have repeated this cross in an attempt to determine the cytological basis of the seeds with maternal endosperms. A maize stock of the composition *a R C pr* was used as the seed parent so that fertilization with Tripsacum which is of the composition *A c r Pr* would result in seeds with purple aleurone while any endosperms which might have developed parthenogenetically would have a colorless aleurone. Material for cytological studies was necessarily collected before the aleurone color had become apparent, but enough preparations were examined to insure that germless seeds and seeds with maternal endosperm were included, provided that these occurred in the same ratios as in the previous experiments.

All of the embryos in which chromosome counts could be made proved to be hybrid embryos, and though the exact chromosome number could not always be determined, it was certain that no embryos with the haploid number, 10, of the maize plant were ever encountered. In the endosperm a few counts were made in which the number was definitely less than 56, the number expected in a hybrid endosperm. In these cases the numbers were usually about 53 (Fig. 30C). The origin of the decreased number of chromosomes is not known. It may have occurred through the loss of a few chromosomes at the time of triple fusion, but it is more likely, we suspect, to have been the result of fusion with Tripsacum gametes containing less than 36 chromosomes. We have already noted that tetraploid Tripsacum forms some multivalents at meiosis and this probably results in slight variations in chromosome numbers among the gametes.

Whatever the cause of the reduced chromosome numbers in some of these hybrid endosperms, it does not seem possible that the slight reduction in number is the cause of maternal endosperm, unless it is always the same chromosomes which are lacking. If the missing chromosomes are a random sample of the Tripsacum chromosome complex, the particular chromosome carrying the allele of the waxy gene would not often be among those lost.

Maternal Endosperm in Crosses with Euchlaena

In 1930 two ears from plants homozygous for sugary endosperm were crossed with Florida teosinte. In both of these ears there was a large number of sugary seeds, and since teosinte is of the composition *Su Su* it appeared that the sugary seeds resulting from this cross were maternal. These two ears bore 298 starchy and 267 sugary seeds, a ratio sufficiently close to a 1:1 Mendelian ratio to suggest that the teosinte plant which had supplied the pollen for this cross may have been heterozygous for the *su* factor as a result of a gene mutation in a previous generation. Fortunately, this assumption can be ruled out on other grounds for these plants were of the genetic composition *AA Cc Rr prpr*. Hence one fourth of the seeds, those receiving both *C* and *R*, should show red aleurone if the endosperm is purely maternal, and purple aleurone if the endosperm is hybrid, for teosinte is of the composition *A c r Pr* (cf. Emerson 1929). Of the starchy seeds on these two ears, approximately one-fourth were colored and all of these were purple, showing that they had received the *Pr* gene from teosinte. Among the sugary seeds, too, approximately one-fourth were colored; but in this group all colored seeds were red. Thus all endosperms which had failed to receive the *Su* gene from teosinte had also failed to receive the *Pr* gene. The natural inference is that all of the sugary endosperms were wholly maternal, the result of parthenogenesis induced by Tripsacum pollen.

Unfortunately, all of the seeds on both ears were germless and incapable of germination. Unfortunately, too, we have never succeeded in reproducing these conditions, maternal endosperm never having been found in our later crosses.

Although we have never succeeded in duplicating the results reported by Collins and Kempton, and have not, in fact, been able to duplicate our own in different seasons, there remains little doubt that induced parthenogenesis does occasionally occur as the result of inter-specific hybridization among the American genera of the Maydeae.

The Genetic Composition of Tripsacum in Aleurone Color Factors

The studies of Emerson (1929) and Emerson and Beadle (1932) have shown that the various forms of teosinte, Durango, Chalco, Florida, and Perennial, are identical in their genetic composition with regard to the four genes usually involved in aleurone colors, and all are of the composition *A c r Pr*. We have made a similar determination of the composition of *Tripsacum dactyloides*, using for this purpose pollen of the Connecticut tetraploid which almost always produces some seeds when applied to the shortened silks of maize. The maize stocks used were of the composition *a C R pr*, *A c R Pr*, and *A C r Pr*, the first stock serving as a tester for both *A* and *Pr*, the other two for *C* and *R* respectively.

Crosses on the first stock produced a few partially developed seeds all of which exhibited purple aleurone, indicating that this form of Tripsacum is of the composition *AA PrPr*.

Crosses on *A c R Pr* produced several good seeds with pronounced endosperm development, all of which exhibited colorless aleurone, indicating that Tripsacum is of the composition *cc*.

Crosses on the R tester *A C r Pr* produced but few good seeds, but several which possessed an endosperm sufficiently well developed to show

Fig. 27. Plant of the triploid hybrid *Tripsacum dactyloides* (2n) X *T. latifolium* (4n). This hybrid is completely sterile.

yellow endosperm color exhibited a colorless aleurone, indicating that Tripsacum is *rr* in composition.

The composition of this form of Tripsacum, *AA cc rr PrPr*, is thus identical with the composition of the different types of teosinte. Additional tests made with *T. latifolium* show that it is of the composition *A A Pr Pr*, but its composition with respect to *C* and *R* has not been determined.

Cytogenetics of Tripsacum Hybrids

T. dactyloides (2n) x T. latifolium (4n)

This hybrid is extremely vigorous, exhibiting a high degree of heterosis (Fig. 27). It is, however, completely sterile; the anthers never dehisce and no seeds have ever been produced from pollinations with either parent. Since sound pollen grains are sometimes found in samples teased from the anthers, we have made a number of pollinations with pollen obtained in this way, all without success.

At diakinesis there are usually 18 bivalents and 18 univalents. The former move to the poles quite regularly and the latter usually lag. There is no way of determining the parentage of the chromosomes involved in the bivalent and univalent bodies; but since *T. latifolium* is a tetraploid form differing in many characteristics from *T. dactyloides* and since trivalents are not usually found, we have assumed that the bivalents represent autosyndesis among the *latifolium* chromosomes and the univalents represent the unpaired *dactyloides* chromosomes.

T. dactyloides (4n) x T. latifolium (4n)

This hybrid, too, exhibits marked heterosis but differs from the preceding one in showing a high degree of fertility. Because of the apparent

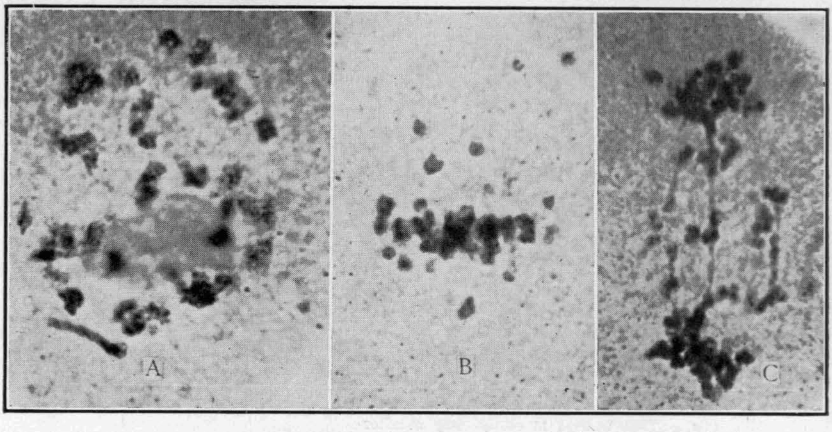

Fig. 28. *Tripsacum dactyloides* (4n) X *T. latifolium* (4n); stages in division-I; X 1400. A. Late prophase. B. Metaphase. C. Late anaphase.

failure of *latifolium* and *dactyloides* chromosomes to pair in the preceding hybrid, we had anticipated that this cross of the two tetraploid forms would result in a true-breeding amphidiploid. Whether this is the case remains to be determined when the variability of later generations is measured. Cytological studies, however, indicate that there will be some segregation, for there are usually unpaired univalents as well as one or two quadrivalents and other irregularities (Figs. 24D, 28A-C).

Zea x T. dactyloides (4n)

Hybrid plants resulting from this cross are usually quite vigorous, although an occasional plant is extremely weak and slow to develop. Some of this variation is shown in Figure 29. We have never found a satisfactory explanation for the stunted plants which occasionally result from this cross. The chromosome number in those in which this has been determined is the same, 46, as in the vigorous plants. Apparently it is a common phenomenon in wide crosses. Mangelsdorf and East (1927) report vigorous and dwarf species hybrids in Fragaria. Venkatraman and Thomas' (1932) illustrations of the hybrids of sorghum and sugar cane show tremendous variability in vigor among the first generation plants. Dekaprelevich (1930) reported great variability in certain hybrids of *Triticum vulgare* and *T. compactum*. Renner (1929) has cited still other examples.

This hybrid, though intermediate between Zea and Tripsacum in its morphological characters, resembles the latter much more closely than the former, a condition probably to be expected since it has received 36 chromosomes from Tripsacum and only 10 from Zea. It is rather strongly perennial and can be maintained indefinitely by vegetative propagation.

Its intermediate condition is strikingly demonstrated in the styles. Both genera have bipartite styles but in Tripsacum the two branches are separated their entire length except at the base; in maize they are fused almost their entire length, a slight split sometimes occurring at the ends. In the hybrid, however, the styles which are considerably longer than those of Tripsacum, averaging 50.6 mm. in length as compared to a length of approximately 25 mm. for those of Tripsacum, are fused for 33.8 mm. or 66.8 per cent of their length. The fusion is so loose, however, that the two parts of the style are easily pulled apart for their entire length.

This hybrid is completely sterile. Anthesis has never occurred and we have never obtained a single seed from the application of either Zea or Tripsacum pollen to the styles, although we have made literally thousands of pollinations.

The embryos and root tips of the hybrids Zea x *T. dactyloides* (4n) usually showed 46 chromosomes (Fig. 30A), and the endosperm 56 (Fig. 30B). These are the theoretical numbers for a true hybrid. However, in the endosperm a few counts were made in which the number was distinctly less than 56, usually about 53 (Fig. 30C).

Fig. 29. Weak plant (left) and vigorous plant (right) of the triploid hybrid Zea x Tripsacum (4n). Both plants have the same chromosome number, 46.

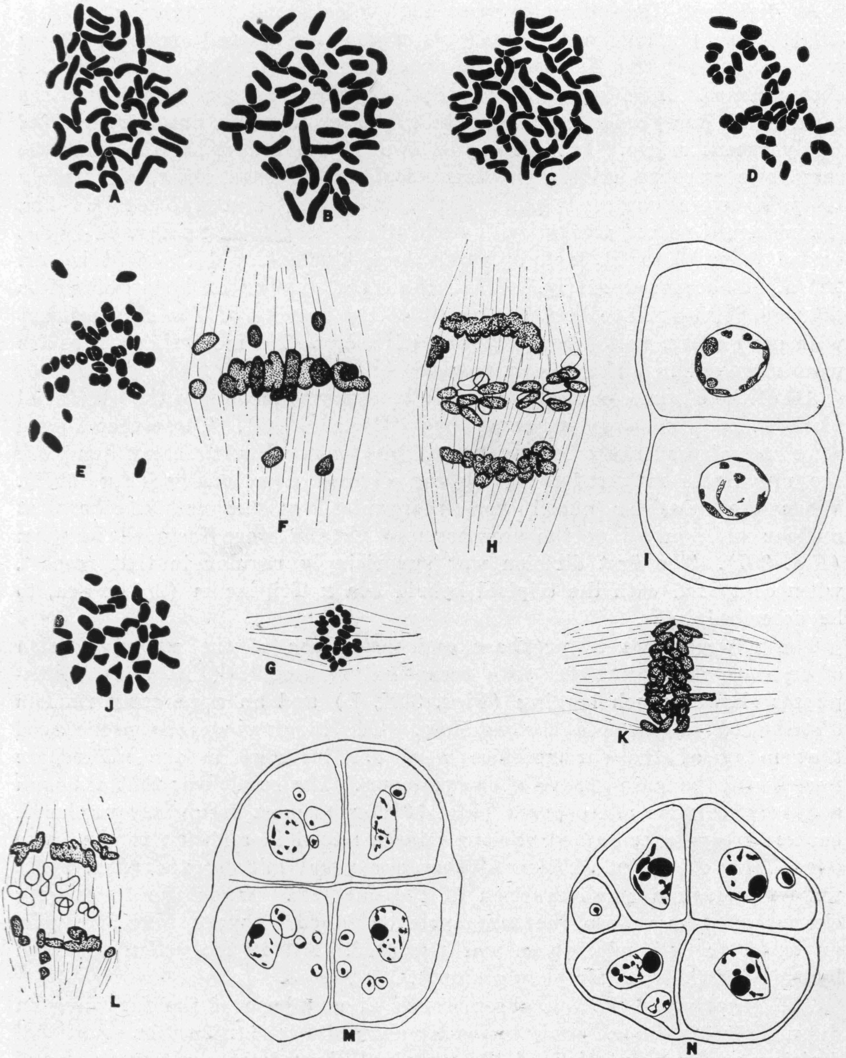

Fig. 30. *Zea mays* **X** *Tripsacum dactyloides* **(4n). A. Root-tip cell; 46 chromosomes; X 2550. B. Endosperm cell; 56 chromosomes; X 2550. C. Same; 53 chromosomes; X 2550. D. Late prophase-I; 18 TT + 10Z; X 1325. E. Same; 18 TT + 1ZZ + 8Z; X 1325. F. Metaphase-I, showing tendency for the Zea chromosomes to lag; X 2550. G. Early anaphase-I; X 1325. H. Later anaphase, showing lagging and equational division of 10 unpaired Zea chromosomes. (The one additional lagging chromosome probably is from Tripsacum); X 2550. I. Apparently regular interphase; X 1300. J. Metaphase-II, showing 28 chromosomes and an additional chromosome or fragment; X 2550. K. Early anaphase-II; X 2550. L. Later anaphase-II, showing lagging and possibly random distribution of 10 Zea chromosomes; X 2550. M. Quartet of microspores, showing supernumerary nuclei that resulted chiefly from lagging in division-II; X 1325. N. Same, showing supernumerary nuclei and a supernumerary microspore; X 1325.**

At diakinesis there usually were 18 bivalents and 10 univalents (Fig. 30D). The pairing in the bivalents was approximately normal. They were assumed to be Tripsacum chromosomes and the 10 univalents Zea chromosomes. This seems to justify our previous conclusion that the form of *T. dactyloides* used in making this cross is an autotetraploid of fairly recent origin. In a few cells two of the univalents of about the same size were seen lying in close proximity to each other, and rarely 19 pairs were observed (Fig. 30E), indicating that two of the Zea chromosomes paired weakly with each other. The total number of bodies varied from 25 to 28, including univalent, bivalent, and trivalent bodies. Trivalents occurred rarely. When the total number of bodies was less than 28, it must have been the result of the pairing of Zea chromosomes with each other, or the formation of trivalents. No more than 28 bodies were observed in diakinesis or metaphase.

All of the chromosomes showed some tendency to move into the equatorial plane at approximately the same time (Figs. 30F, G). Those that lagged were univalents or the loosely paired bivalents. During early anaphase the univalents frequently lagged and divided equationally (Fig. 30H). When the daughter nuclei were reorganized at the end of the first nuclear division all of the chromosomes usually were included in them (Fig. 30I). The first division was surprisingly regular in that respect, when compared with the triploid hybrid Zea x Tripsacum (2n) x Zea, to be described later.

The chromosomes in prophase and metaphase of the second division often were 28 in number, with occasional fragments (Fig. 30J). Anaphases showed much lagging (Figs. 30K, L) and an apparently random distribution of the Zea chromosomes. The lagging was so pronounced that many of the chromosomes were not included in the microspore nuclei with the main groups of chromosomes. The result was that although a quartet of four microspores (Fig. 30M) was most frequently produced, each microspore contained various minute nuclei in addition to the large one. Microcytes, in addition to the four usual microspores (Fig. 30N) were found in a small fraction of the quartets. When the 10 lagging chromosomes moved to the same pole or failed to move to either pole, an extra or fifth microspore was produced. All of the pollen produced by this hybrid was completely empty.

The behavior of the Zea chromosomes at anaphase of the first division did not receive enough study to justify a definite conclusion that equational division or fragmentation of the unpaired chromosomes always occurred in the first meiotic cell division. But this phenomenon sometimes was observed, and two other types of observations are in agreement with this view. (1) Counts of chromosomes at metaphase of the second division usually showed 23 to 28 chromosomes rather than the average of 23 that would be expected on the opposite assumption. (2) A small number of observations were made incidentally from second anaphase figures that indicate a random distribution of 10 chromosomes at this time. These observations are recorded in Table 3. Numbers were tabulated only

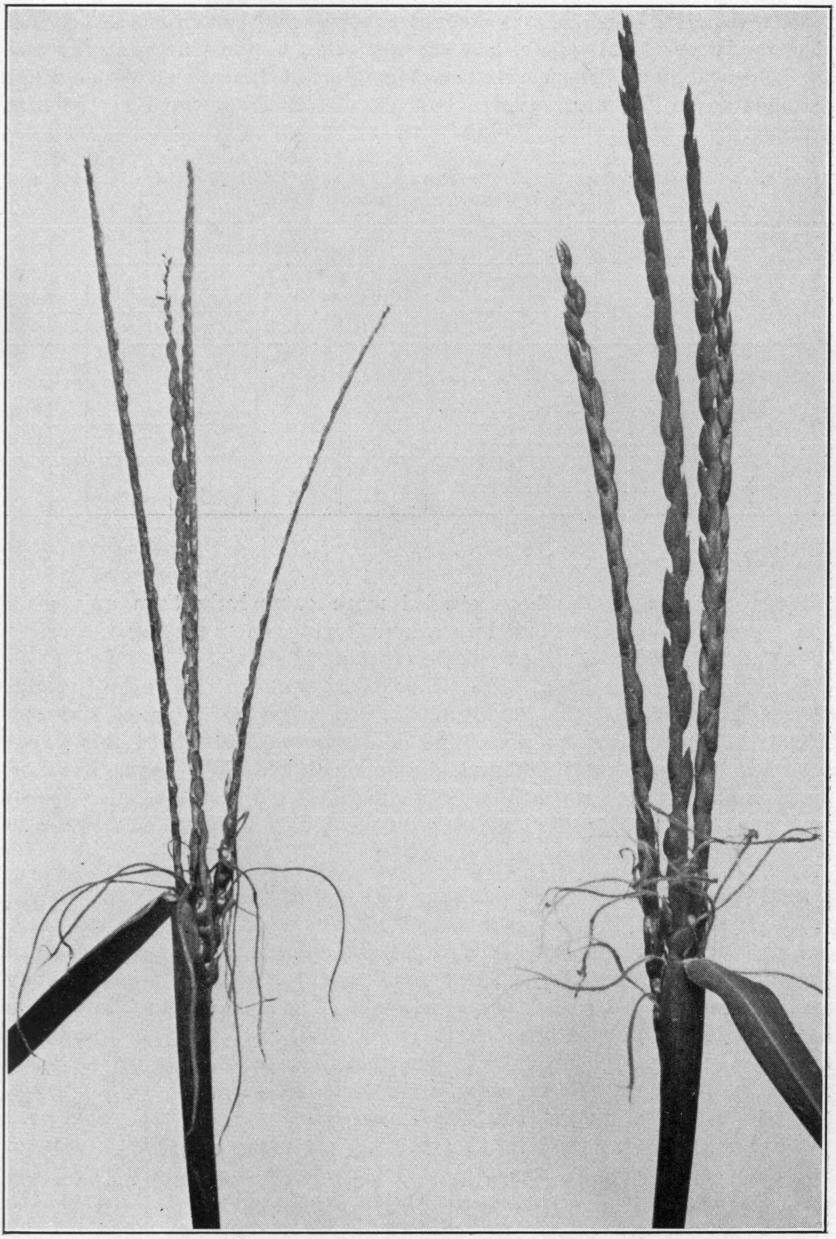

Fig. 31. Terminal inflorescences of the diploid hybrid Zea X Tripsacum (2n) and the triploid hybrid Zea X Tripsacum (4n). Note longer styles in first hybrid and split ends of styles in second.

from those cells in which two distinct groups could be recognized on each side of the equatorial plane, one group moving to the pole normally and the other lagging. The chromosomes lagging at the second division are assumed to be Zea chromosomes that divided or fragmented at the first division.

Table 3. Distribution of lagging chromosomes at the second meiotic division in the hybrid *Zea mays* x *Tripsacum dactyloides* (4n)

Slide number	Distributions involving					
	10 chromosomes					Other numbers
	0 & 10	1 & 9	2 & 8	3 & 7	4 & 6	5 & 5	5 & 3
296 A–1	....	....	1	4	6	2	....
296 A–2	....	....	....	2	4	4	....
296 D–1	....	....	....	....	....	1	1
Totals	....	....	1	6	10	7	1
Expected: random distribution	....	....	2	5	9	5	0

Zea x T. dactyloides (2n)

Since this hybrid has been studied more extensively than any other and because it has contributed to a new hypothesis regarding the origin of maize, the studies involved will be reported in detail.

The technique used in hybridizing these genera has already been described in considerable detail in an earlier paper (Mangelsdorf and Reeves 1931) and briefly mentioned in a previous section of this paper so that it needs no additional discussion here. We have, however, made some rather extensive studies of the development of the hybrid fruits; and since they have never been previously recorded it may be in order to present these at this point.

Development of the Hybrid Seeds: When the structure of the mature fruits of Zea and Tripsacum is compared, a similarity is seen; but there are striking differences. An idea of the difference in size may be obtained by comparing Figures 33A and D, both of these representing approximately mature grains and drawn to the same scale. The endosperm of Tripsacum has a more pronounced basal stalk (Figs. 33D, 35I) than Zea, and this seems to be regularly present. It has been described in Zea by Weatherwax (1930), Lampe (1931), and Randolph (1936) as a conducting tissue. Our study of the structure of the Tripsacum grain has not progressed far enough to justify a detailed report at present, but apparently there are other differences in minute structure between the caryopses of Zea and of Tripsacum. Twenty-nine hours after pollination some of the hybrid proembryos were two-celled and these were accompanied by endosperms having 32 nuclei. In other pistils that had been pollinated for the same period there was no sign of division of either the zygote or the primary endosperm nucleus. The Zea embryos showed about the same range of variation. While no division of either zygote or primary endosperm nucleus had occurred in 29-hour ovaries,* divisions had occurred in some of the 21-hour ovaries of Zea as well as the hybrid (Fig. 34A). This may be explained best as natural fluctuations in growth. In general, variation in rate of growth of the Zea proembryos and endosperm seem to be about the same as in those of the hybrid.

Fig. 32. A successful pollination with Tripsacum (2n). Some ears set seeds almost 100 per cent. The hybrid seeds, however, are very small compared to maize seeds of the same age. The larger seeds near the middle are the result of pollinating with maize 24 hours after pollinating with Tripsacum. Note that some of the hybrid seeds adjacent to the maize seeds are larger than their sibs.

Thirty hours after pollination the hybrid proembryo consisted of two to four cells (Figs. 34B, C), and in four-celled proembryos of this age the apical cell had been divided by a vertical wall. In a few proembryos a tier of three cells with parallel cross walls were formed before vertical

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*For convenience, the expressions 29-hour ovaries, 32-hour embryos, etc. are applied to organs that were fixed 29 hours, 32 hours, etc. after pollination. Since there is variation in the time elapsing between pollination and fertilization, it is considered best to calculate ages from the time of pollination, which is definitely known in this material.

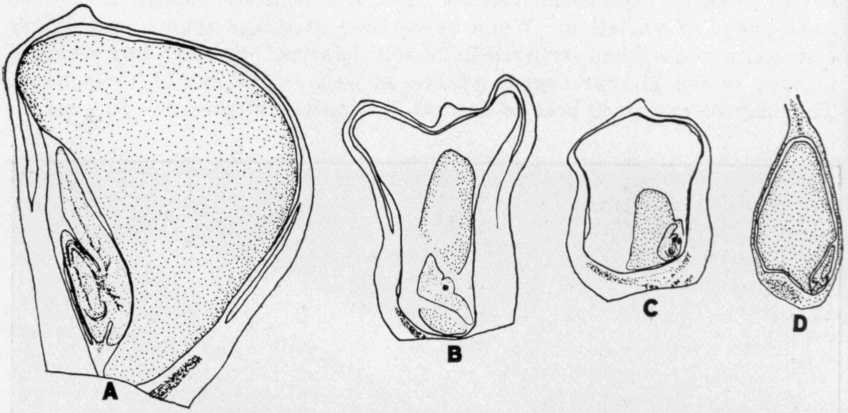

Fig. 33. **Almost mature ovaries containing embryos and endosperms of *Zea mays*, *Tripsacum dactyloides* (2n), and F_1 hybrids; X 6. A. *Zea mays*. B, C. F_1 hybrids. D. *Tripsacum dactyloides*. A, B, and C are from the same maize ear.**

walls developed, but this probably was not true of the majority of them. In all proembryos examined, however, the first wall formed was approximately horizontal. Figures 34A to F give an idea of the structure of the hybrid embryos up to 75 hours after pollination.

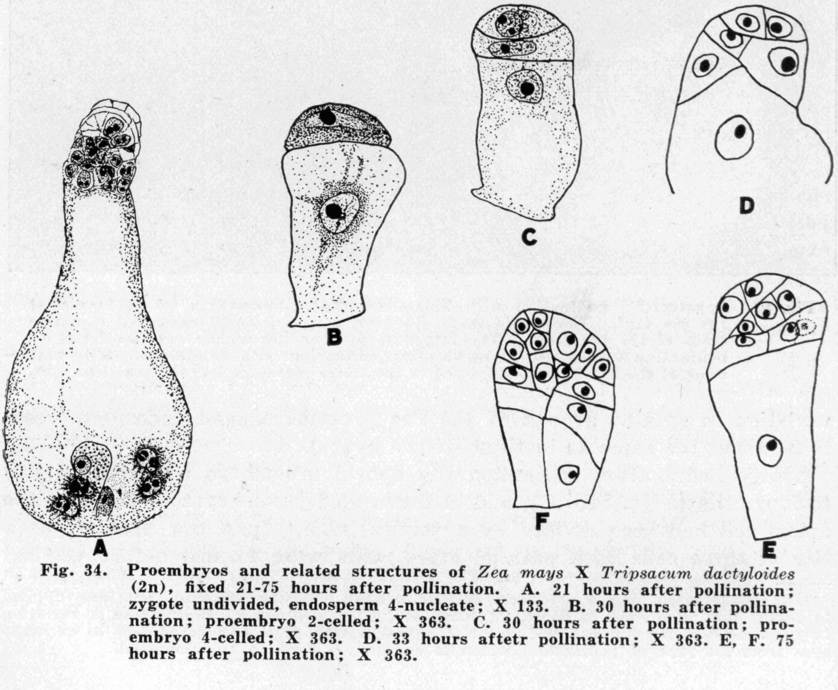

Fig. 34. **Proembryos and related structures of *Zea mays* X *Tripsacum dactyloides* (2n), fixed 21-75 hours after pollination. A. 21 hours after pollination; zygote undivided, endosperm 4-nucleate; X 133. B. 30 hours after pollination; proembryo 2-celled; X 363. C. 30 hours after pollination; proembryo 4-celled; X 363. D. 33 hours aftetr pollination; X 363. E, F. 75 hours after pollination; X 363.**

The cellular condition of the hybrid endosperm was seen to appear soon after the 128-nucleate condition was passed, or between 36 and 75 hours after pollination. No cellular endosperms were observed in ovules as young as 36 hours, and no free nuclei were seen at 75 hours or after. Starch was always present in 11-day, and sometimes in 7-day, endosperms. The division of the endosperm nuclei tended to occur in unison, but probably never was the unison perfect. It was not uncommon to find the nuclei in the micropylar end of the embryo sac in metaphase and those in the antipodal end in the metabolic condition. The divisions begin in the micropylar end, and the activity spreads to the antipodal end. The unison becomes less pronounced in older endosperms, and after the cellular condition is reached, it can scarcely be detected.

The development of hybrid embryos thus far is quite similar to the normal development in Zea embryos, as described by Randolph (1936), except that the rate of development of the hybrids is a little more rapid. The average 30-hour hybrid embryos correspond approximately to the 32- and 36-hour Zea embryos, and the most advanced 30-hour hybrid embryos (Fig. 34C) are in the same condition as the least advanced 42-hour embryos of Zea. The 33-hour hybrid embryos (Fig. 34D) correspond approximately to the most advanced 42-hour Zea embryos and to some of the 4-day (96-hour) Zea embryos. The 75-hour hybrid embryos (Figs. 34E, F), are more advanced than the 4-day (96-hour) embryos of Zea.

A statistical study would be required to determine definitely whether the average rate of development in the hybrids exceeds that of Zea, but there is a very strong indication that in young ovaries the most rapidly developing hybrid embryos exceed the most rapidly developing embryos of Zea.

An examination of Tripsacum pollen germinating on Zea stigmas showed a wide variation in the rate of germination and in the rate of pollen tube growth. This is some indication of the variation to be expected in the hybrid embryo and suggests that the variation is not necessarily genic or chromosomal, since the pollen and hybrid embryos are about equally uniform in genes and chromosomes. The more rapid development of the hybrid embryos may be explained by climatic differences, as the Zea embryos described by Randolph developed under New York conditions, and those of the hybrid under Texas conditions. Also, varietal differences in the maize used in each study, and hybrid vigor may have influenced the rate of development. The fact that our pollinations with Tripsacum were made on shortened styles seems to have little bearing on this difference, since pure Zea embryos developing from normal pollinations began their development almost as early as the hybrids (Table 4). Before an attempt is made to determine which, if any, of these causes is the correct one, a study of the rate of development of the Tripsacum embryo should be made.

Table 4. Rate of early development of embryo and endosperm of Zea and the hybrid Zea x Tripsacum (2n)

Parentages of seeds	Period after pollination	Condition of			
		Embryo		Endosperm	
		Least advanced	Most advanced	Least advanced	Most advanced
Zea 1229-19	21 hours	no division	no division	no division	4-nucleate
Zea x Tripsacum 1231-15	21 hours	no division	no division	no division	4-nucleate
Zea 1229-19	29 hours	no division	no division	no division	no division*
Zea x Tripsacum 1231-8	29 hours	no division	2-celled	no division	32-nucleate
Zea x Tripsacum 1225-31	30 hours	2-celled	4-celled	32-nucleate	64-nucleate
Zea x Tripsacum 1226-28	33 hours	8-celled	11-celled	32-nucleate	128-nucleate
Zea x Tripsacum 1226-28	36 hours	3-celled	6-celled	128-nucleate	128-nucleate
Zea x Tripsacum 1228-14	75 hours	15-celled	32-celled	multicellular+	multicellular+
Zea x Tripsacum 1228-15	5 days	60-celled	multicellular+	multicellular+	multicellular+
Zea x Tripsacum 1228-15	7 days	multicellular+	multicellular+	multicellular+	multicellular+†
Zea x Tripsacum 1232-17	11 days	multicellular+	multicellular+	multicellular+	multicellular+‡

*Fertilization had occurred in some of the ovules but not in all of them.

†No differentation of organs of embryo was observed.

‡Differentiation of organs of embryo had occurred in a few ovules.

+The term "multicellular" is applied here only to structures estimated to have more than 150 cells.

This variation in rate of development was found to continue until the grain was approximately mature, but only rarely did an unusually rapid rate continue after the 14th day. The most advanced 11-day hybrid embryos showed differentiation of the scutellum, plumule, and radicle (Fig. 35A), but others of the same age showed no differentiation (Fig. 35B).

All 14-day embryos examined showed some differentiation, and in most of them obvious abnormalities were detected (Figs. 35C, D). The abnormalities were of various kinds and are difficult to classify. A common type consisted of an oblique orientation of the axis (plumule and radicle) with reference to the scutellum (Fig. 35D). More extreme abnormalities are shown in Figure 35C, in which the radicle and scutellum were lacking or extremely abnormal. The latter was abnormally oriented and was imbedded in a large cavity of the endosperm. In other ovaries, the embryo and endosperm were reduced in size and showed indications of atrophy.

In 16-day ovaries similar abnormal conditions were apparent. In Figure 35F the embryo was in such a position that it separated the endosperm into two parts, the main bulk of the endosperm being above and a small portion below. The scutellum was in contact with the smaller, lower part of the endosperm. The axis of the embryonic plant was oriented almost crosswise to its normal position. No well defined radicle was present in this embryo. The embryo shown in Figure 35E is only slightly abnormal.

For the purpose of comparison, illustrations A to D in Figure 33 were drawn to the same scale and, with the exception of the pure Tripsacum, represent ovaries taken from the same ear, this ear having been pollinated first with Tripsacum and 24 hours later with Zea. Three distinct size classes of grains were developing on this ear, the largest being the result

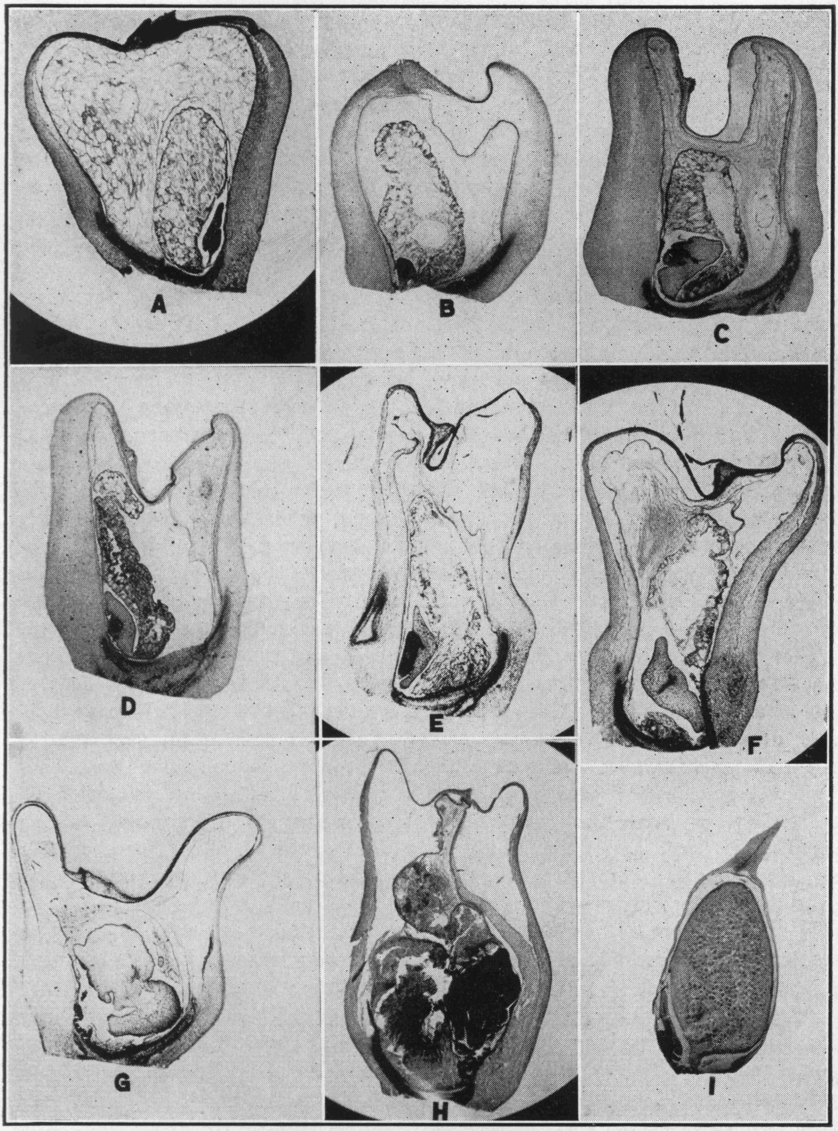

Fig. 35. A-H Ovaries containing embryos and endosperms of *Zea mays* X *Tripsacum dactyloides* (2n), fixed 11-21 days after pollination; X 7. A, B. 11 days after pollination; A. approximately normal in structure but reduced in size. C, D. 14 days after pollination. E, F. 16 days after pollination. G. 20 days after pollination. H. 21 days after pollination. I. Approximately mature caryopsis of *T. dactyloides* (2n); X 7.

of the pollination with Zea. Of the two types of hybrid embryos, one (Fig. 33B) was abnormal in several respects (see description of Fig. 35F, and the other (Fig. 33C) was much reduced in size. The hybrid embryos were 16 days old and the Zea 15 days when collected.

In most of the hybrid grains 16 days old, and often older, there was still a large non-cellular region near the center of the endosperm. Randolph (1936) states that in 4-day Zea endosperm this portion is usually cellular. This region gives the endosperm of these hybrids a tendency to collapse when placed in fixing agents, but only slight shrinkage occurred in the best of the material used. The large cavities shown in the structures external to the endosperm occur naturally, for they were regularly observed before the material was placed in the fixing agent. The small embryo and endosperm simply did not fill the large ovary of Zea in which they were developing.

At 20 and 21 days after pollination the embryos that were still alive usually had replaced a considerable portion of the endosperm and had attained fair sizes (Figs. 35G, H), although the embryo often was extremely abortive, as in Figure 35G. In a few ovaries of these ages, the endosperm still contained large central non-cellular regions which were abnormal for such advanced stages, but embryos of approximately normal structure (Fig. 35H). The endosperm of the hybrid seeds seldom attained more than half the size of that of Zea, and usually much less than half. This resulted in a pronounced shrivelling of the pericarp.

There was a definite tendency for embryos and endosperms taken from the same ear, and therefore having the same parentage, to show similar abnormalities. Grains from a certain ear (1228-3 x 4-1) characteristically showed a peculiar, narrow, crescent-shaped endosperm that tended to lie along the basal end and along the side of the embryo sac. This type of abnormality was not found elsewhere. The abnormal embryo and endosperm from the cross 1229-26 x 3-6 and most of the other ovaries taken from that ear were similar; in fact some of them were almost indistinguishable from each other, and similar structures were not found on other ears. Observations of this kind were made many times.

In a few ovaries, endosperm but no embryo was present. In two ovaries the embryos had been almost completely resorbed, and this may be the explanation of the apparent lack of embryos in some of the other ovaries. However, in a single instance, an ovary five days after pollination showed 16 free nuclei in the endosperm and no sign of egg, zygote, or proembryo. The chromosome number could not be determined in the endosperm nuclei as none of them were dividing. Whether this development of endosperm was parthenogenetic is therefore unknown. The other ovaries from the same ear and of the same age showed several hundred cells in both endosperm and embryo.

It was impossible to predict which of these abnormal grains would sprout when planted, but it was obvious that many of them would not; because their embryos, when present, did not possess the primordia of the vegetative organs of the plant. It was shown, however, that many of the slightly abnormal grains did have the potentiality to sprout and produce healthy plants; for nearly all of the seeds showed some structural abnormalities and the percentage of germination, although small, was certainly greater than the percentage of seeds that showed no structural abnormality.

It is generally recognized that there are critical periods in the lives of plants, and one of these, at least in hybrids, is the time when the differentiation of organs of the embryo begins (cf. Brieger 1928).

Another factor which may be involved in the failure of the hybrid seeds is their inability to stimulate a flow of nutrient materials into the growing ear. We have frequently observed that when only a few hybrid seeds occur the entire ear is very likely to shrivel. If the ear is well filled with hybrid seeds, it is much more likely to continue growth; but even under these conditions, there is a decided tendency for the latent lateral branches of the plant to develop as they usually do when the upper ear has not been pollinated. If, however, the ear bears a few true corn seeds in addition to the hybrid seeds, it behaves more like a normal ear. Furthermore, hybrid seeds adjacent to normal corn seeds are frequently larger and better developed than hybrid seeds growing alone (Fig. 32). In fact, hybrid seeds adjacent to corn seeds average about 40 per cent heavier than hybrid seeds on the same ears but at a distance from the corn seeds. This may suggest that the normal corn seeds are capable of stimulating a flow of nutrient materials into the region which they occupy, benefiting the adjacent hybrids which are not capable of inducing a stimulus of the same degree. Whether or not this is a sound interpretation, there is no doubt that the presence of normal corn seeds is an effective stimulant to the development of the hybrid seeds.

Michurin (1936), who has observed a similar effect in Rubus crosses, is of the opinion that some species and genera are difficult to cross because the scent of the foreign pollen is an obstacle to fertilization. He recommends mixing the foreign pollen with three times as much maternal pollen so that the former will acquire part of the scent of the latter. Though his premise is probably wrong, the method has been successful. Beasley (unpublished) has also used the method of mixed pollination with some success in cotton species hybrids. We suspect that the failure of hybrid seeds to develop in many species crosses is due less to the inherent weakness of the hybrids than to their inability to stimulate a flow of nutrient materials into the region which they occupy. Perhaps this accounts for the success which Laibach (1929) and others have had in culturing the partly grown hybrid embryos in artificial media.

But even with the use of double pollinations, the percentage of hybrid seeds which reach maturity is very small. In 1930 we exposed to pollination by Tripsacum approximately 185,000 silks on 382 ears. Approximately 36,000 seeds were set, of which 84 reached maturity, a ratio of 4.54 seeds to each 10,000 ovules pollinated. Of the 84 mature seeds, 45 germinated when grown on sterile agar after removal of the pericarp and

Fig. 36. Plant of the hybrid Zea X Tripsacum [2n] (right), compared with its maize parent (left).

treatment with one of the organic mercury fungicides (Mangelsdorf and Reeves 1931) and 29 plants survived transplanting to the field.

The Hybrid Plants: The majority of the hybrid plants finally obtained were quite vigorous but there was some variation and several plants were decidedly weak and stunted. One of the normal plants is shown in Fig. 36; one of the stunted plants in Fig. 37. The chromosome numbers are the same in both. It will be recalled that a similar variation in the vigor of the hybrid plants occurred in the cross of Zea x tetraploid Tripsacum (see p. 89).

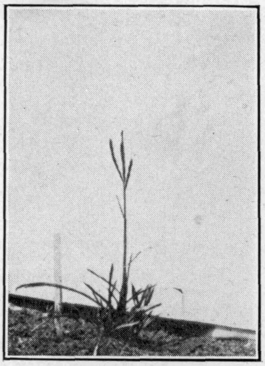

Fig. 37. Weak, stunted plant from the cross Zea X Tripsacum (2n). This plant has the same chromosome number as the vigorous hybrid illustrated in Fig. 36 and is photographed to the same scale.

The hybrid of Zea x *T. dactyloides* (2n) like that of Zea x *T. dactyloides* (4n) resembles Tripsacum more closely than it does Zea, at least in general appearance (Figs. 36 and 38). Actual quantitative measurements show, however, that the resemblance to Tripsacum is by no means as marked as in the preceding hybrid. For example, the hybrid of Zea x tetraploid Tripsacum is strongly perennial and can be maintained indefinitely by vegetative propagation. The hybrid of Zea x diploid Tripsacum is only weakly perennial and is difficult to propagate in this way.

Cytology: Counts of the chromosomes were made in root tips, embryos, and endosperms (Figs. 39A, B). Whenever definite numbers could be determined, they corresponded exactly with the theoretical numbers; that is, in root tips and embryos the number was 28, in the endosperms it was 38.

During the first meiotic division the degree of pairing of chromosomes in late prophase was variable. It was rarely possible to find a cell in which there was obviously no pairing, but in some instances there was doubt that a single pair was present. When pairing did occur it was feeble, except for two or three pairs which had a tendency to unite more closely and regularly (Fig. 40A). A few cells having the various numbers of pairs were tabulated and the results were: no pairs, 0; one

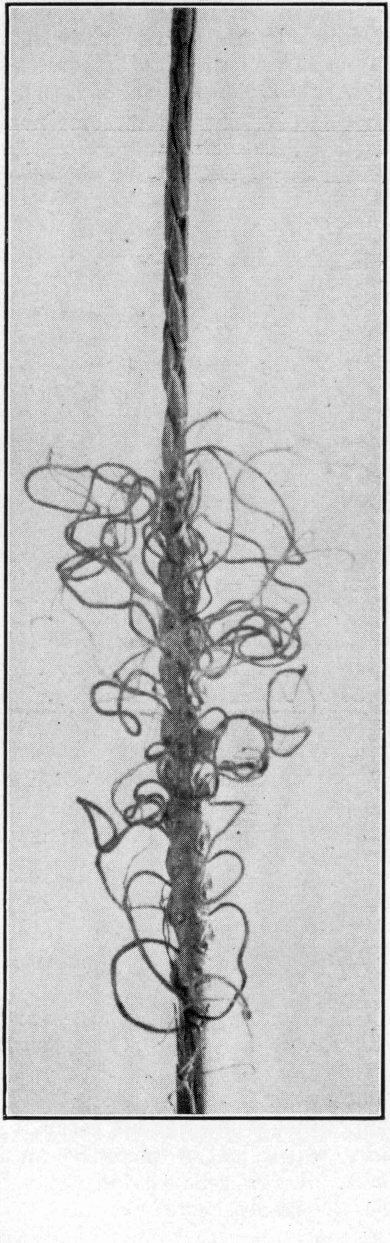

Fig. 38. Lateral inflorescence of the hybrid Zea X Tripsacum (2n) with enveloping leaf sheath removed. Note tangled silks. The combination of a Tripsacum-like spike, with long silks and enveloping leaf sheaths is a "disharmonious" one.

Fig. 39. Chromosome numbers in embryo and endosperm of *Zea mays* X *Tripsacum dactyloides* (2n); X 2550. A. The 28 chromosomes of the embryo. B. The 38 chromosomes of the endosperm.

pair, 2; two pairs, 5; three pairs, 21; four pairs, 21; five pairs, 8; six pairs, 1.

During the prophase, the chromosomes shortened but there was a tendency for them to remain longer and less compact than in the parent plants where pairing was more regular. Their affinity for carmine was also less pronounced than when normal pairing occurred. A regular metaphase figure was never observed but, instead, the chromosomes remained more or less scattered over the central portion of the cell. In a few preparations there was, however, a tendency for them to form something of a row across the equatorial plane (Fig. 40B). This tendency seemed to be peculiar to certain plants; it was noted particularly in No. 282-1, but in nearly every cell examined of such plants the number of lagging chromosomes was greater than the number on the metaphase plate. Whenever counts could be made, the numbers corresponded fairly closely to 10 on the equatorial plane and 18 lagging, although seldom were these the exact numbers. The chromosomes that came into the equatorial region frequently divided. The lagging chromosomes that did not come into

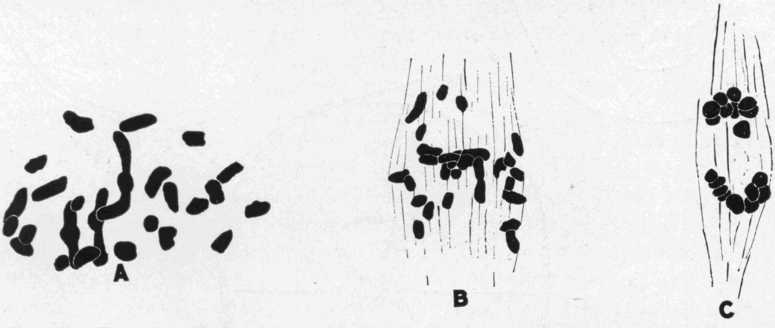

Fig. 40. *Zea mays* X *Tripsacum dactyloides* (2n); prophase to anaphase of division-I; X 1325. A. 22 univalent and 3 bivalent chromosomes. B. One definitely bivalent chromosome and several doubtful ones. C. Anaphase of fairly regular appearance.

the equatorial plane were simply included in the nucleus to be formed at the poles near where they happened to be located. These facts suggest that in certain plants the Zea chromosomes, or many of them, divide at the first division and the 18 Tripsacum chromosomes are distributed at random.

Anaphases consisted of all types of behavior from an apparently regular anaphase (Fig. 40C) to a phenomenon in which there was no movement of chromosomes towards the poles. The latter behavior affords a means by which unreduced female gametes, which these plants often produced, may be formed. When the chromosomes failed to move towards the poles, a definite nuclear membrane was finally formed around them at or near the center of the cell. The partition wall that formed following this failure of nuclear division sometimes was located entirely to the side of the newly constructed restitution nucleus (Fig. 41A). A secondary microsporocyte, such as the one including the nucleus, would therefore produce a diad of microspores each having the unreduced number of chromosomes.

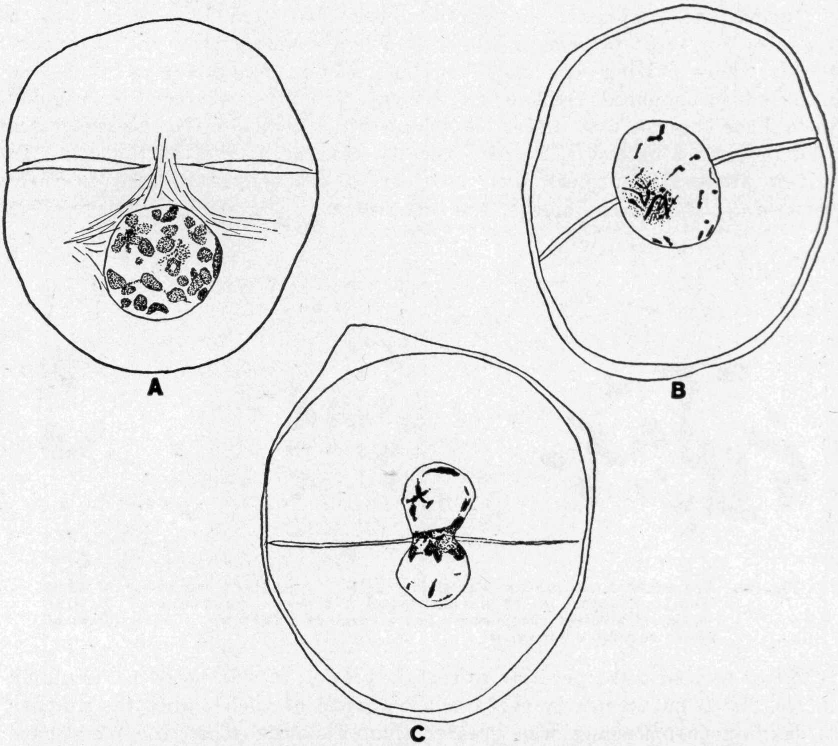

Fig. 41. *Zea mays* **X** *Tripsacum dactyloides* **(2n); restitution nuclei; X 1325. A. Restitution nucleus wholly within one of the daughter protoplasts. B. Restitution nucleus apparently extending through the partition wall. C. Same, giving appearance of being constricted by partition wall.**

A cytological condition of similar character was found in which the partition wall was formed in such a position that it was in contact with the equatorial portion of the nucleus (Fig. 41B). Cells have been seen in which the nucleus had the appearance of being constricted by the partition wall (Fig. 41C). Whether this constriction's being caused by the partition wall was only apparent or real is uncertain at present, but it probably was only apparent. The partition walls of pollen mother cells of *Zea mays* have been shown by Reeves (1928) to develop centrifugally. For the partition wall to constrict the nucleus, which in this material was near the center of the cell, would require some different mode of development. Probably the chromosomes included in such nuclei had undergone a phenomenon similar to the bridging often observed in abnormal mitoses; and thus the nuclear membrane, which merely outlined the group of chromosomes, formed in such a manner as to give the nucleus the shape of a dumb-bell, such as was shown by McClintock (1938), to be the result of the fusion of broken ends of sister half chromatids following chromatid breakage.

When the first anaphase occurred, the distribution of chromosomes was random except among those that arranged themselves on the metaphase plate and divided equationally. When chromosome counts could be made in both members of a pair of secondary sporocytes, the numbers again showed the amount of splitting at the first anaphase. Assuming no splitting or fragmentation, the total number of bodies in the two secondary sporocytes should be 28; all above that number must have occurred by splitting or fragmentation. In most pairs of secondary sporocytes the total number was greater than 28 (Fig. 42B). There was a pronounced tendency for the chromosomes to divide during the prophase of the second division, but care was taken to distinguish between divided and undivided chromosomes and to record counts only from those cells in which splitting appeared not to have occurred.

The behavior of the chromosomes during the second division depended somewhat upon the type of phenomenon that occurred during the first. When the nucleus was reconstructed without a first nuclear division in such a manner that it lay partially in each of the two secondary sporocytes, as in Figures 41B, C, the row of second metaphase chromosomes apparently extended through the cell wall (Fig. 42C). The completion of the second division in cells of that type probably gave a quartet of normal appearance (Fig. 42D). Abnormally oriented spindles (Fig. 42E) and structures, such as are shown in Figures 42F and G, were not uncommon.

It would seem that plants of those groups whose quartets of microspores are formed by a simultaneous furrowing process would stand a better chance of producing unreduced pollen than those whose quartets are formed by two successive divisions, such as the grasses. In the former, a partition would never be present in which the restitution nucleus may become so "entrapped" that portions of its chromosomes would be on opposite sides of the partition, as in Figures 41C and 42C.

When the splitting of the second division chromosomes is completed,

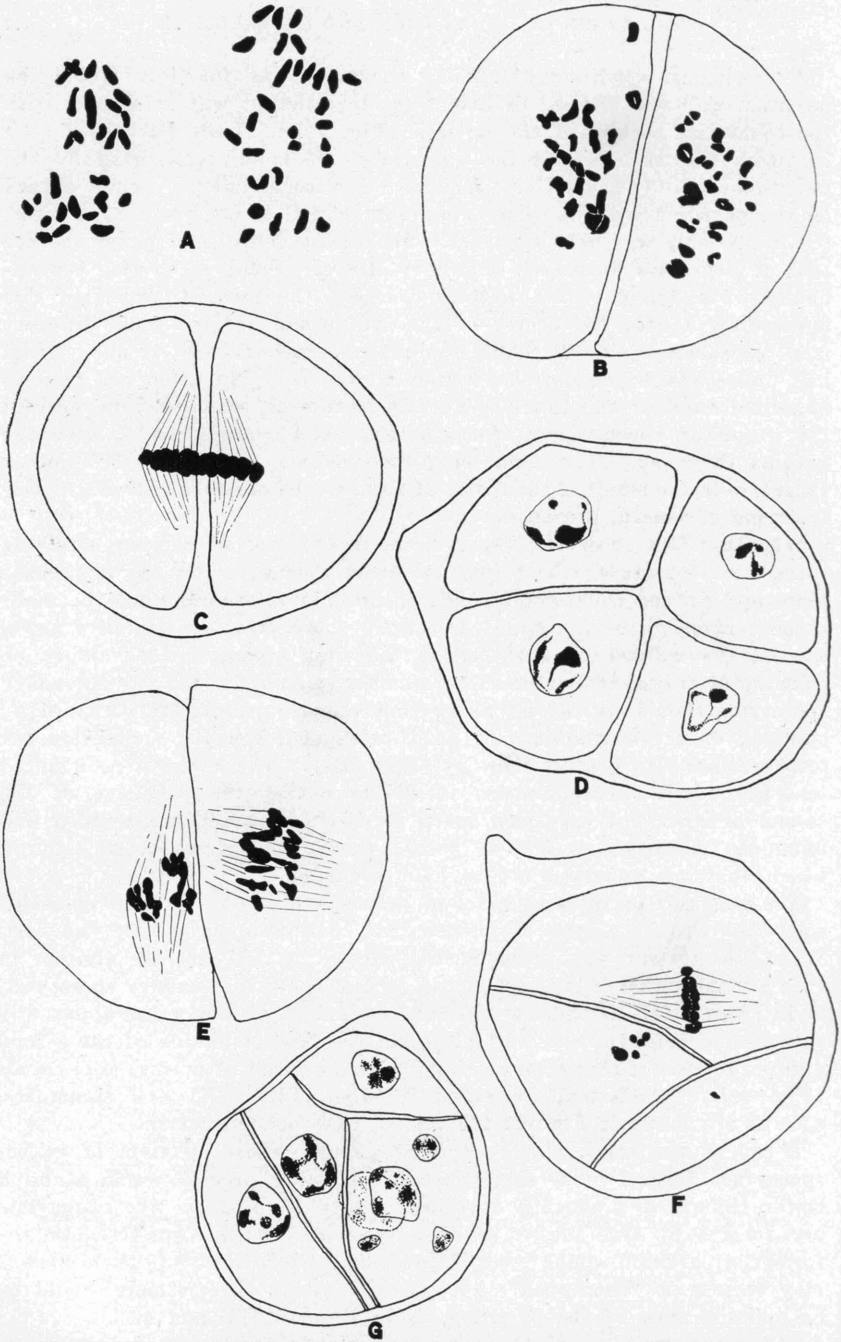

Fig. 42. *Zea mays* X *Tripsacum dactyloides* (2n); division-II; X 1325. A. Chromosomes of sister secondary sporocytes, one sporocyte showing 29 chromosomes and the other 27. B. Secondary sporocytes; prophase of division-II. C. Metaphase of division-II; a condition resulting from the omission of division-I, such as occurs in Fig. 41 B and C. D. Apparently regular quartet, such as may follow metaphases similar to C. E. Abnormally oriental spindles of secondary sporocytes. F, G. Other abnormalities.

the two daughter cells should show a total of 56, assuming that the halves resulting from an equational splitting in the first division are distributed at random in the second and that the chromosomes that were distributed at random in the first division divided equationally in the second. Whenever counts could be made, there was a fair agreement with this assumption (Fig. 42A), but fragmentation of chromosomes increased the number of bodies in some instances.

The hybrid is completely pollen-sterile. In most plants the anthers fail to dehisce; and in the few plants from which pollen has been shed, all the grains are completely empty. This is rather surprising, for the formation of unreduced gametes has been observed cytologically, and the plants are partially fertile on the pistillate side, exhibiting a fertility of 1.3 per cent when pollinated with diploid Tripsacum, 3.4 per cent when pollinated with Zea, and 5.8 per cent when pollinated with Euchlaena. It is probably due to the fact that the proportion of functional pollen grains is so small that the entire anther fails to develop normally, or because the hybrid sporogenous tissue is incapable of bringing these particular gametic combinations to maturity, in spite of their favorable chromosome constitution. As Renner (1929) in writing of a similar situation stated: "Ein Teil der Gonen mag schon unverträgliche chromosomensätze haben, der Rest geht trotz günstiger Konstitution der Genome zugrunde."

Most of the functional egg cells, probably all of them, carry the unreduced chromosome number. This is shown by one of the hybrid plants which was heterozygous for the gene *Y* for yellow endosperm received from its maize parent. Pollinated with a white-seeded maize *yy* it produced only yellow seeds. Unless all maize chromosomes are included in all functional gametes, white seeds should occasionally result from this pollination, for the chromosome bearing the *Y* gene is as likely to be omitted as any other.

The Triploid Hybrid (Zea x Tripsacum-2n) x Zea

Cytological observations and genetic results had indicated that the only functional gametes produced by the diploid hybrid Zea x Tripsacum (2n) were unreduced. Thus when this hybrid was crossed back to Zea the result should have been a triploid hybrid possessing two genoms of Zea and one of Tripsacum. A population resulting from this pollination was, furthermore, expected to be rather uniform, for all plants should be of the same genomic constitution, ZZT, where Z represents a genom from Zea and T a genom from Tripsacum.

This has proved to be the case. Chromosome counts made from the root tips of the triploid hybrids consistently showed 38 chromosomes (Fig. 45A), the theoretical number expected from combining two Zea genoms of 10 chromosomes each with one Tripsacum genom of 18. Occasionally a plant appeared to have a slightly smaller number, such as 36 or 37; but these lower numbers were never definitely verified, and

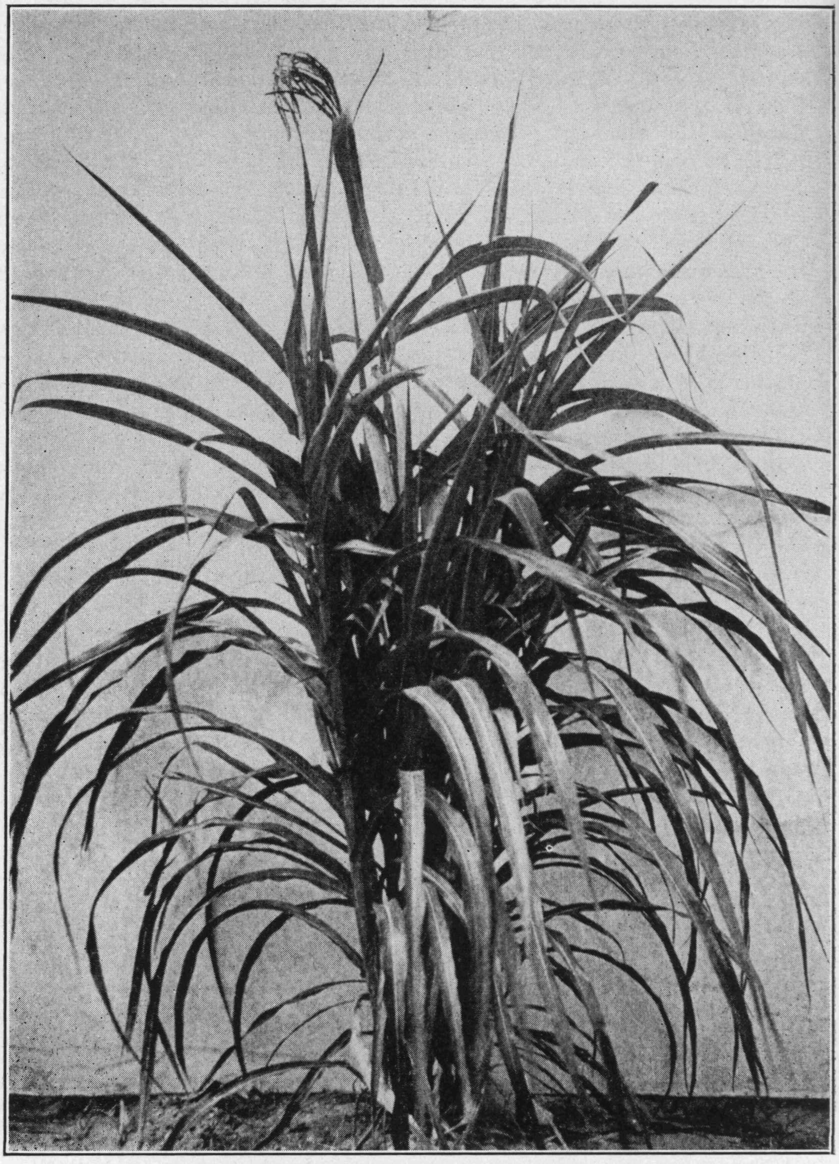

Fig. 43. Plant of the triploid hybrid (Zea X Tripsacum) X Zea. This plant posesses 38 chromosomes comprising two genoms of 10 chromosomes each from Zea and one genom of 18 from Tripsacum.

the fact that the plants were quite uniform in their various vegetative characteristics would indicate that all possessed the same chromosome complex.

The Hybrid Plants: This triploid hybrid exhibits a superficial resemblance to *Euchlaena mexicana* in its vegetative characteristics (Fig. 43). It tillers rather profusely but the tillers are much coarser than those of Tripsacum and more like those of Euchlaena. Like Euchlaena, too, it is a long-lived annual, but short days are not required to bring it into flower. It differs from the two Zea x Tripsacum hybrids previously described in possessing a central spike in the tassel and in bearing only staminate spikelets in the terminal inflorescence. The lateral inflorescences are covered with shucks, and at first glance appear to be small but normal ears of maize. When the shucks are removed, however (Fig. 44), the influence of Tripsacum is at once apparent in the presence of staminate spikelets, prominent horny glumes, and a tendency for the segments of the rachis to disarticulate. The greater influence of Zea, as compared to that in the preceding hybrids, is apparent in the higher percentage of pistillate spikelets on the lateral inflorescence, and in the paired condition of the spikelets. Paired pistillate spikelets are occasionally found in the hybrid Zea x Tripsacum (2n) but these are the exception rather than the rule. In this hybrid they are the rule. The distichous arrangement of spikelets characteristic of Tripsacum continues to be dominant and this combined with the pairing of the spikelets results in an ear that is distinctly four-rowed. The distichous arrangement is no longer so completely dominant, however, for occasional ears with three and even four double rows of spikelets are found; and since the spikelets are always paired, this results in six- and eight-rowed ears. Of 60 ears examined from 9 plants, 8 were six-rowed, 4 were eight-rowed, and the remaining 48 were four-rowed. The six- and eight-rowed ears all occurred on the same plants with four-rowed ears, indicating that there is a rather delicate balance between the distichous and polystichous condition in this hybrid which is easily thrown in one direction or the other by environment.

The average number of tillers is 6.2, number of leaves 85; number of tassel branches 10.7, and number of ears 12.8.

Cytology: Diakinesis figures showed 10 paired and 18 unpaired chromosomes, except that in most cells one or several trivalents were found. The trivalents are believed to be the result of a feeble union of a Tripsacum chromosome with a pair of Zea chromosomes. The number of trivalents varied, but usually at least one pair was found. Metaphase and anaphase figures of the first division showed one (Fig. 45B), two (Fig. 45C), three, or four (Fig. 45D) trivalents. It is a fact, possibly of significance, that all of the unpaired or feebly paired Tripsacum chromosomes often came into the equatorial region with the paired Zea chromosomes. When this occurred, the individual chromosomes usually could not be distinguished. This may be interpreted as meaning that the average number of trivalents

Fig. 44. Lateral inflorescence of the hybrid (Zea x Tripsacum) x Zea. This spike has the paired spikelets of Zea but resembles Tripsacum in its distichous arrangement, fragile rachis, prominent horny glumes, and presence of staminate spikelets.

formed was somewhat greater than that usually observed. Cells were observed in which the Tripsacum chromosomes showed a slight tendency to pair among themselves (Fig. 45B). In many such cells, difficulty was experienced in determining whether there was an association between two chromosomes or whether they were merely lying in contact. But in the best preparations, in which the cells were well pressed by the cover glass so that the chromosomes were spread apart, a connection between two chromosomes other than those already discussed rarely could be seen. Also, in anaphase figures loosely connected chromosomes were found that could be interpreted either as two members of a trivalent passing to a pole or as two loosely paired Tripsacum chromosomes that had not moved to the metaphase plate (Fig. 45E). Such bodies probably are best considered to be two members of the trivalent passing to a pole, because paired chromosomes would be expected to move to the metaphase plate even if the pairing is weak. At anaphase, fragmentation of chromosomes and bridging of those on the equatorial plane (Fig. 46A) were not uncom-

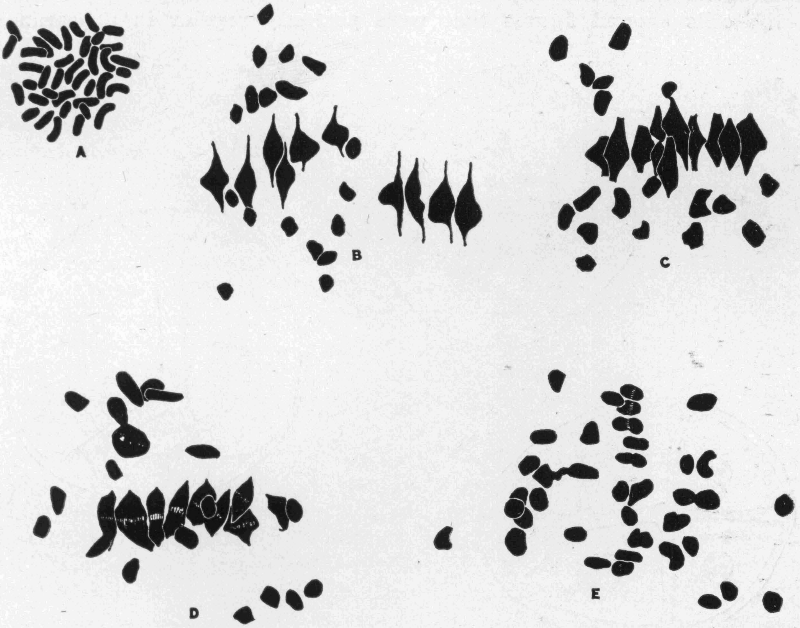

Fig. 45. (*Zea mays* X *Tripsacum dactyloides* - 2n) X Zea; somatic chromosomes and early stages of meiosis. A. Root-tip cell; 38 chromosomes; X 1700. B. Division-I, showing 9 ZZ chromosomes, 17 T chromosomes, and 1 ZZT chromosome, (drawn in two parts); X 1700. C. Same, showing 8 ZZ chromosomes, 16 T chromosomes, and 2 ZZT chromosomes; X 1700. D. Same, showing 6 ZZ chromosomes, 14 T chromosomes, and 4 ZZT chromosomes; X 1700. E. Later stage; a sporocyte which probably contained 2 trisomes in earlier stages, as the 2 bivalents probably have disjoined from the third member; univalents in metaphase position showing tendency to divide; disjoined members of bivalents moving towards poles; X 1700.

mon. The unpaired Tripsacum chromosomes sometimes came onto the equatorial plane and showed signs of division. They apparently divided or fragmented after exhibiting the bridging phenomenon, or divided in a fairly regular way, but more often they moved to the poles undivided.

Telophase figures (Fig. 46B) often show two large nuclei and various numbers of small ones. The small nuclei usually contained from one to three chromosomes or fragments.

Metaphase of the second division showed that the chromosomes of the small nuclei had a tendency to move onto the equatorial plane, for many of the cells showed figures that were perfectly regular in appearance.

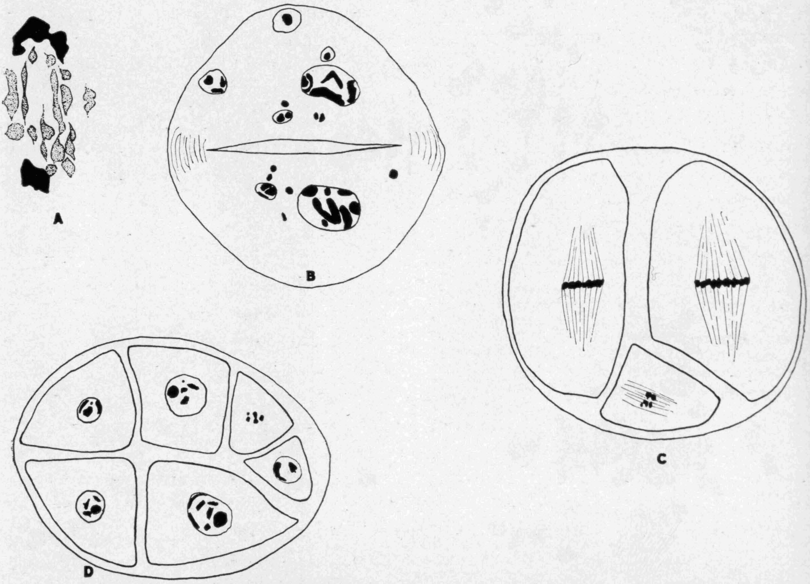

Fig. 46. (*Zea mays* X *Tripsacum dactyloides* - 2n) X Zea; late stages in meiosis; X 833. A. Sporocyte near completion of division-I showing bridging and lagging of light-staining chromosomes. B. Completion of nuclear division-I, showing supernumerary nuclei. C. Metaphase-II, showing supernumerary cell. D. Abnormal unit of microspores.

Irregularities usually were found, however, in which microcytes had been separated off by partition walls at the end of the first division (Fig. 46C). Groups of extremely irregular structure (Fig. 46D) were much more common than the regular quartets.

This hybrid, like all preceding ones discussed, is completely pollen-sterile but it shows a rather high degree of fertility when pollinated by Zea. A total of 1,758 pollinations produced 374 seeds. This represents a fertility with Zea of 21.3 per cent. Pollinations of 410 silks with pollen from *T. dactyloides* (4n) and 420 with pollen from *T. dactyloides* (2n) produced not a single mature seed, though in both cases aborted seeds were produced in small numbers.

A Comparison of Diploid and Triploid Hybrids of Zea and Tripsacum with the Parental Genera

Three hybrids of Zea and Tripsacum have now been described—the first a triploid hybrid of Zea x Tripsacum (4n), the second a diploid hybrid of Zea x Tripsacum (2n), and the last a triploid hybrid (Zea x Tripsacum) x Zea. With respect to the genoms received from Zea and Tripsacum these hybrids are of the constitution ZTT, ZT and ZZT. Combined with the two parental genera they constitute a series of five forms in which the percentage of Zea germplasm varies from 0 to 100. A comparison of these forms in various morphological characteristics, in which the two parents differ by wide extremes, should be of interest from several standpoints.

First, it should show whether the two genera are differentiated by dominant genes. Edgar Anderson (1936) has pointed out this possibility in a similar comparison which he was able to make in hybrids between *Tradescantia subaspera* and the diploid and tetraploid forms of *T. canaliculata.* With respect to the genoms involved, four types were available for comparison—CCCC, CCSS, CSS, and SSSS, in which the letters C and S represent single genoms from *canaliculata* and *subaspera* respectively. Since there were striking differences between the two hybrids, he concluded that the genic differences between the two species were largely without dominance.

A second question which may be asked from this comparison is whether a genom of Tripsacum is equivalent to a genom of Zea, or whether it is the individual chromosomes which are equivalent to each other. This question is raised because Tripsacum has 18 chromosomes, Zea only 10. The discovery of a chromosome number of 9 in Manisuris, a genus formerly classified as a species of Tripsacum, suggests that the form of Tripsacum which we have been calling the diploid, may, in reality, be a tetraploid. Thus if Zea and Tripsacum originally possessed approximately the same number of genes, the present diploid Tripsacum would now have almost twice as many genes as Zea. In this case a Tripsacum genom would, theoretically, have more influence on the hybrid than a Zea genom. In terms of percentages of Zea and Tripsacum genoms and Zea and Tripsacum chromosomes, the three hybrids and their parents have the composition shown in Table 5.

Table 5. The composition of Zea x Tripsacum and their diploid and triploid hybrids with respect to percentage of genoms and percentage of total chromosomes from each genus

Parent or hybrid	Number genoms from		Per cent Zea	Number chromosomes		Per cent Zea
	Tripsacum	Zea		Tripsacum	Zea	
Tripsacum	2	0	0	36	0	0
Zea x Tripsacum (4n)	2	1	33.3	36	10	21.7
Zea x Tripsacum (2n)	1	1	50.0	18	10	35.7
[Zea x Tripsacum (2n)] x Zea	1	2	66.7	18	20	52.6
Zea	0	2	100.0	0	20	100.0

There are a large number of characteristics in which Zea and Tripsacum differ (Figs. 47-50), which might be measured in comparing these two genera and their hybrids; but as it is impossible to provide all forms with an identical environment, since their time of flowering is

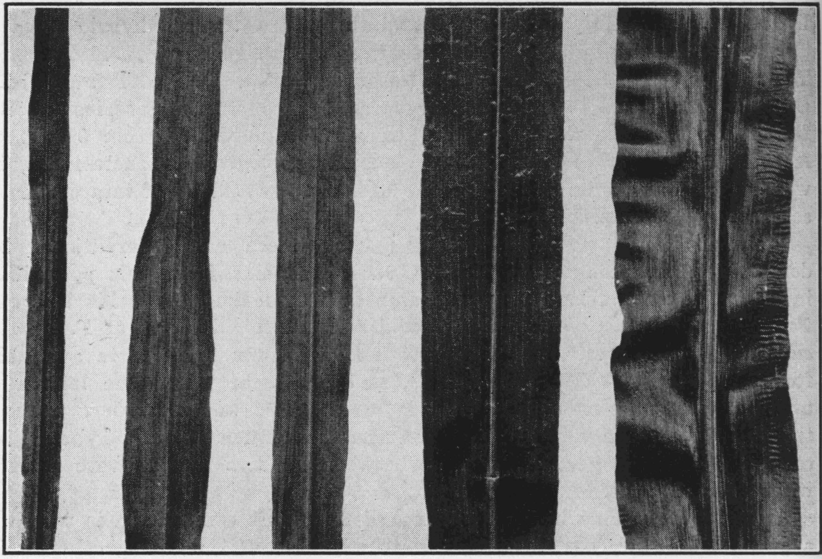

Fig. 47. Leaves of Tripsacum and Zea and their three hybrids. Number of veins per unit of width decreases with an increase in percentage of Zea germ plasm.

Fig. 48. Staminate spikelets of Tripsacum and Zea and their three hybrids. Note increase from left to right in length of pedicels and prominence of pubescence.

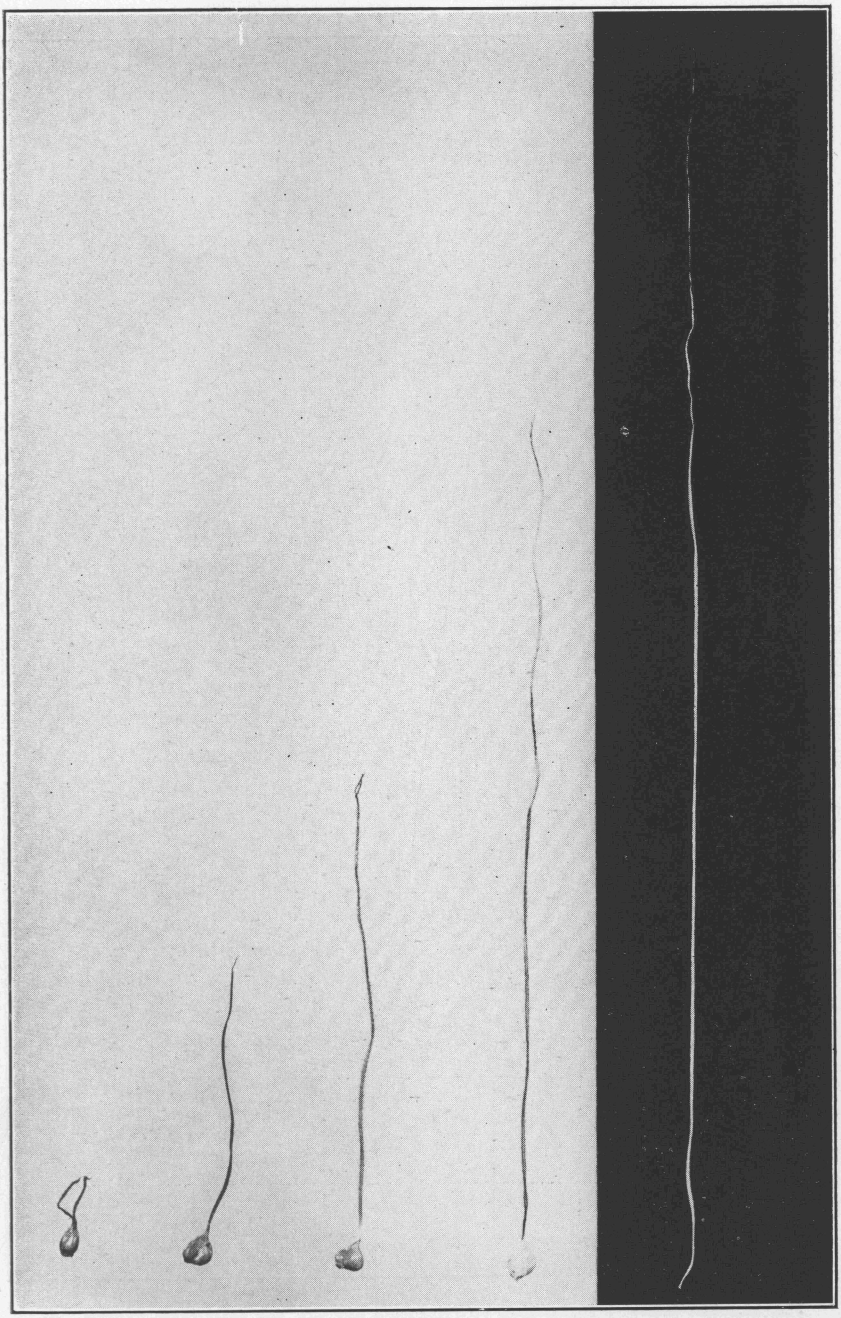

Fig. 49. The styles of Tripsacum and Zea and their three hybrids. From left to right the genomic constitution is TT, TTZ, TZ, TZZ, ZZ.

Fig. 50. The lateral inflorescences of Tripsacum and Zea and their three hybrids. Note increase in proportion of pistillate spikelets which accompanies increase in percentage of Zea germ plasm.

so different, we have selected several characteristics which are not greatly affected by environment, providing that it does not deviate too widely from the optimum. To counteract still further the effects of differing environments, we have made measurements over a period of several years and have used the averages of these in making comparisons.

In order to make possible a direct comparison between different characteristics, we have converted all quantitative measurements into terms of percentages. For example, the average length of styles in Tripsacum is 14.0 mm., in Zea 184.3 mm., in the three hybrids, 50.6 mm., 84.0 mm., and 151.4 mm. In terms of percentage, so that Tripsacum was always recorded 0 per cent and Zea 100, the length of styles in Tripsacum which contains no Zea germplasm, is 0; in Zea, which contains 100 per cent of Zea germplasm, the length is 100. The relative length of styles in the three hybrids now becomes 21.5, 41.1 and 80.7.

This procedure not only permits a direct comparison between different characteristics but it allows us to arrive at an average value for all characteristics of any one hybrid, an average of all hybrids for any one characteristic, and finally an average of all characteristics of all hybrids. The data so obtained must be interpreted in one of six ways as follows:

If a genom of Zea is equivalent to a genom of Tripsacum, and there is no dominance, the relative values for any particular characteristic, or the averages for all of them, will approach 33.3, 50.0, and 66.7 in the three hybrids and the average of these three values will approach 50. If there is a partial dominance of the Tripsacum genes, the values will be lower than this in each case, and will approach zero as the lower limit. If there is a dominance of Zea genes, the values will be higher in each case and will approach 100 as the limit.

If it is the individual chromosomes which are equivalent rather than the genoms, the relative values of the three hybrids, in the absence of dominance, should be 21.7, 35.7 and 52.6, with an average of 36.7. Partial dominance of Tripsacum genes would cause these values to be lower in each case; dominance of Zea genes would result in higher values in each case.*

A glance at the data in Table 6 will show that four of the six possible interpretations can be immediately eliminated. The average value for all three hybrids in the three characters measured is 49.6, which is very close to the value of 50 expected if the genoms are equivalent and there is no pronounced dominance of either parent. We cannot be dealing with a situation where the chromosomes of Tripsacum are equivalent to those of Zea either with partial dominance or no dominance of the Tripsacum genes, for either of these conditions would result in an average value much below 50. Dominance of Tripsacum with the genoms equivalent to each other would also result in a value below 50, while dominance of Zea under these conditions would yield a value above 50.

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*All of these computations assume that physical units of equal size measure biological units of equal value. Rasmusson (1933) and Sinnott (1937) have shown that this is not always true. For the purpose of this discussion, however, the assumption seems reasonable.

There remain but two interpretations to be considered—one that the Tripsacum and Zea chromosomes are equivalent, with a pronounced dominance of Zea genes; the other that Zea and Tripsacum genoms are equivalent, with no consistent dominance of the genes of either genus. Since the former interpretation would call for average values lying anywhere between 36.7 and 100 and since the latter can result only in a value of 50, the fact that an actual value of 49.6 was obtained, speaks very strongly in favor of the second interpretation. It would be a coincidence, indeed, if Zea exhibited a partial dominance of exactly the right degree to counterbalance the larger number of Tripsacum chromosomes.

The fact that the average values of the three hybrids approach a linear relationship (Fig. 51) also speaks against a dominance of Zea genes for such a situation would result in a curvilinear relationship. We can conclude, therefore, that it is the genoms rather than the chromosomes of the two genera which are equivalent, and that neither genus exhibits appreciable dominance, when all of these particular characteristics are considered together.

This same situation occurs in the observations which we have made on a number of qualitative characteristics in which the two genera differ and in which quantitative measurements are difficult or impossible to make. These are listed in Table 7. These observations indicate a slight dominance of Tripsacum in some characteristics, a slight dominance of Zea in others, and an intermediate condition in the remainder. The dominance of one parent over the other has, however, never been marked in any of the characters under study. In horniness of glumes, for example, the observations indicate that Tripsacum is completely dominant in this characteristic, for the glumes are horny in all combinations in which Tripsacum genoms occur. If horniness could be measured quantitatively, however, it could undoubtedly be shown that the degree of horniness varies with the percentage of Tripsacum germplasm and that dominance is by no means complete. The same is true of the pedicels on the second male spikelet. The pedicel is present in all combinations which contain Zea germplasm, but the length of the pedicel varies directly with the proportion of Zea germplasm (see Fig. 48).

The presence or absence of the central spike of the tassel is an interesting characteristic, for no intermediate condition has ever been observed in our experiments. It is always absent in Tripsacum; always present in Zea. The fact that it is absent in the diploid hybrid might indicate that Tripsacum is the dominant parent so far as this characteristic is concerned. But the dominance is certainly not complete, for the triploid hybrid with two genoms of Zea and one of Tripsacum possesses a central spike in the tassel. In characters such as this we are, apparently, dealing not so much with dominance as with balance and a threshold point.

Table 6. Comparison of diploid and triploid hybrids of Zea and Tripsacum with the parental genera in several quantitative characteristics

Parent or hybrid	Composition	Per cent Zea		Number veins per cm.		Length styles, cm.		Per cent ♀ florets on laterals		Average relative values
		Genoms	Chromosomes	Actual	Relative	Actual	Relative	Actual	Relative	
Tripsacum	TT	0	0	9.2	0	14.0	0	9.4	0	0
Zea x Tripsacum (4n)	TTZ	33.3	21.7	7.0	39.3	50.6	21.5	14.8	5.9	33.2
Zea x Tripsacum (2n)	TZ	50.0	35.7	5.3	69.6	84.0	41.1	23.3	15.2	42.0
[Zea x Tripsacum (2n)] x Zea	TZZ	66.7	52.6	3.7	98.2	151.4	80.7	47.9	42.0	73.6
Zea	ZZ	100.0	100.0	3.6	100.0	184.3	100.0	100.0	100.0	100.0
Average of three hybrids	....	50.0	36.7	....	69.0	....	47.8	....	21.0	49.6

Table 7. Comparison of diploid and triploid hybrids of Zea and Tripsacum with the parental genera in qualitative characters

Character	Genomic composition of parent or hybrid				
	TT	TTZ	TZ	TZZ	ZZ
Central spike in tassel	absent	absent	absent	present	present
Paired vs. single ♀ spikelets	single	single	single +	paired	paired
Two rows ♀ spikelets vs. many rows	two	two	two	two-four	four-many
Horny vs. membranaceous glumes	horny	horny	horny	horny—	membranaceous
♀ spikelets in tassel	present	present	present	absent	absent
Brittle vs. solid rachis	brittle	brittle	brittle	sl. brittle	solid
Pedicel on second spikelet	sessile	pedicelled	pedicelled	pedicelled	pedicelled
Growth habit	perennial	perennial—	annual +	annual	annual

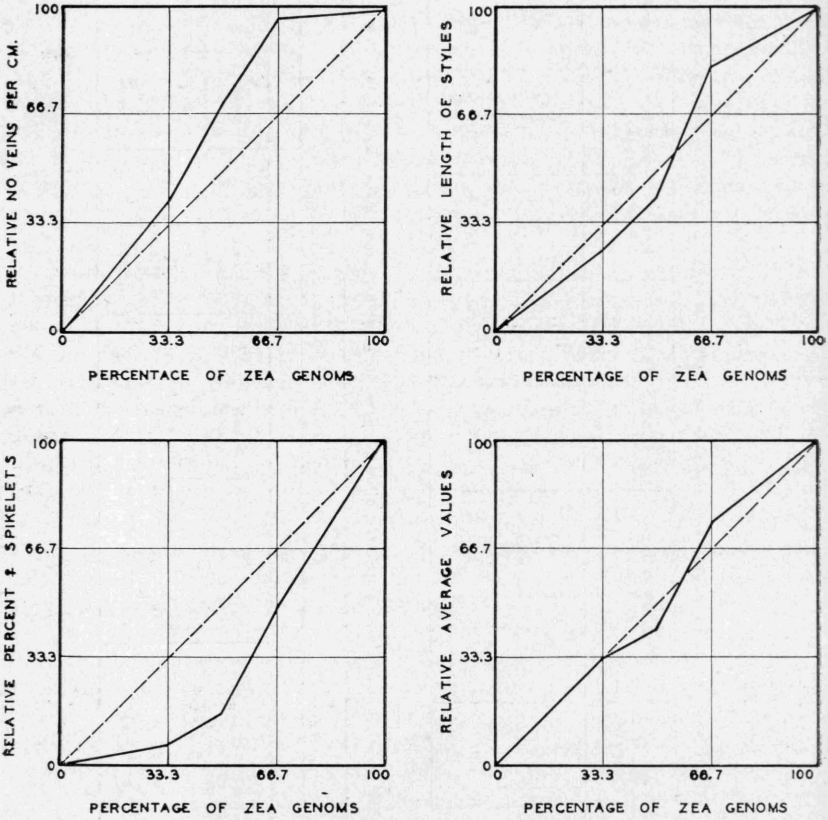

Fig. 51. The relation between percentage of Zea genoms and the expression of quantitative characteristics by which Zea and Tripsacum differ.

The Trigeneric Hybrid of Zea, Tripsacum, and Euchlaena

The feasibility of producing a triple hybrid combining all the chromosomes of the three American Maydeae, Zea, Tripsacum, and Euchlaena, suggested itself immediately when the cytology of the hybrid Zea x Tripsacum (2n) was studied (p. 103), for these studies showed that unreduced gametes carrying one genom each of Zea and Tripsacum were regularly formed. By pollinating this hybrid with Euchlaena, therefore, it should be possible to produce a triploid hybrid which is not only trigeneric but also trigenomic, combining all of the chromatin of all three genera. This has proved to be the case, and the trigeneric hybrid resulting from this pollination has already been described in a previous paper (Mangelsdorf and Reeves 1935), and hence we shall review the results but briefly here.

The diploid hybrid Zea x Tripsacum is fully as fertile when pollinated by the third genus, Euchlaena, as when pollinated by either of its parents.

In fact, the percentage of fertility exhibited in this pollination, 5.8 per cent, is higher than that obtained from pollinations with either Tripsacum or Zea. This may be due to the fact that the latter pollinations were made in the field and the former in the greenhouse; but there is also a possibility, to be discussed in detail later (p. 203), that Euchlaena is itself a mixture of genes from Zea and Tripsacum and hence might well be expected to cross more readily with a Zea x Tripsacum hybrid than would either of the parental genera. In any case, there was no difficulty in crossing the hybrid Zea x Tripsacum with Euchlaena, and from 208 ovules pollinated, 12 good seeds were obtained. The resulting offspring were quite uniform.

Inheritance of Parental Characters in the Hybrid: A comparison of the characteristics of the hybrid with its three parents is set forth in Table 8. Naturally, it is impossible to make a strictly accurate comparison among the four types of plants involved because their growing season is so different. All that we have attempted to do is to make observations and measurements of the three species and their hybrid when they were at comparable stages of development. Our classification of the characteristics studied as "qualitative" and "quantitative" is purely arbitrary, though the former can, in general, be described by observation, the latter only by measurement.

Table 8. Characteristics of Zea, Euchlaena, Tripsacum, and their triple hybrid

Character	Zea	Euchlaena	Tripsacum	Triple hybrid
Growth habit	annual	annual	perennial	annual
Root stocks	absent	absent	present	absent
Central spike in tassel	present	absent	absent	absent
Secondary tassel branches	absent	present	absent	absent
Pedicels on second male spikelet	pedicelled	pedicelled	sessile	pedicelled
Female spike enclosed in husks	enclosed	enclosed	naked	enclosed
Branching of lateral inflorescence	present	present	absent	present
No. rows functional pistillate spikelets	many	two	two	two
Brittleness of rachis	solid	brittle	brittle	brittle
Seeds enclosed in shell	naked	enclosed	enclosed	enclosed
Average number tillers	0.1	6.5	19.0	6.0
Average width of leaves, cm	5.4	4.8	1.0	6.0
Average number nerves per cm	3.5	4.2	8.1	4.0
Average number branches per tassel	14.4	18.9	3.0	6.4
Average number staminate florets in tassel	462.0	1512.0	274.0	334.0
Average number pistillate florets in tassel	0.0	0.0	18.0	1.4
Per cent pistillate florets in tassel	0.0	0.0	6.6	0.4
Average number ears	1.8	165.0	95.0	41.0
Average number ovules per ear	485.0	5.7	9.6	14.2
Average length of styles, mm	233.0	76.0	14.0	99.0
Percentage of length styles are fused	99	99	0.0	94.9
Days, planting to blooming	95.0	210.0	210.0	192.0

Though the hybrid clearly exhibits characteristics of each of its three parents, it shows a greater resemblance to Euchlaena than to either of the other two component genera (Figs. 52-55). This resemblance is so striking that, from the taxonomic standpoint, the hybrid, if it occurred in nature, would probably be classified as a species of Euchlaena. It

Fig. 52. The trigeneric hybrid (Zea X Tripsacum) X Euchlaena. This plant possesses 38 chromosomes comprising one genom of 10 from Zea, one genom of 10 from Euchlaena, and one genom of 18 from Tripsacum.

Fig. 53.—Lateral inflorescences of the trigeneric hybrid (Zea X Tripsacum) X Euchlaena. This spike is essentially identical with that of pure teosinte, even to the presence of partially developed staminate spikelets at the tip.

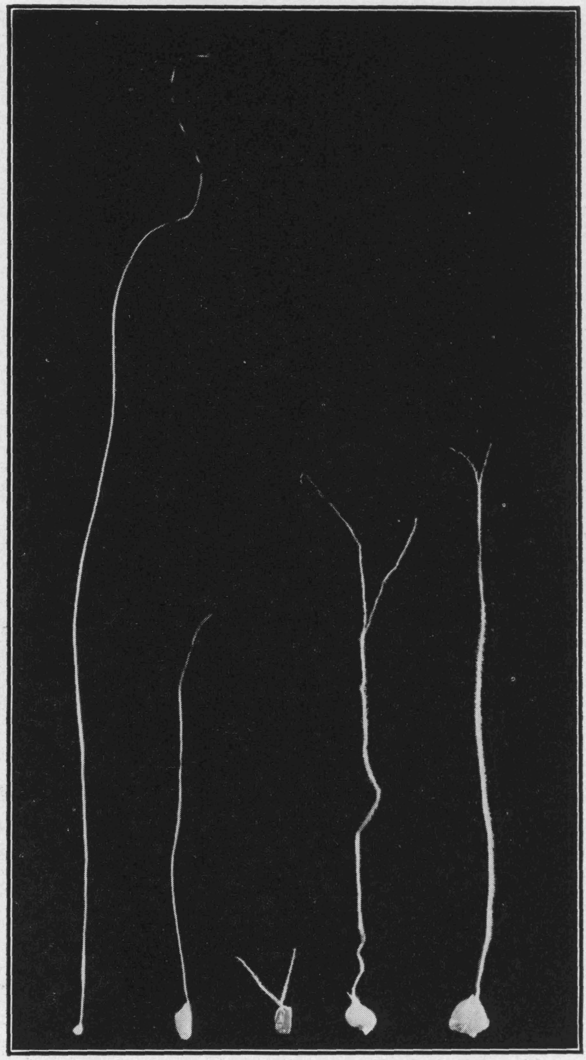

Fig. 54. Variation in length and structure of styles. From left to right, Zea, Euchlaena, Tripsacum, Zea X Tripsacum, (Zea X Tripsacum) X Euchlaena. Note influence of Tripsacum in partial splitting of silks in both hybrids.

resembles Euchlaena in all of the qualitative characters considered except one—the presence of secondary branches in the tassel—and approaches this genus in a number of quantitative characters including the number of nerves per cm., number of tillers, percentage of pistillate spikelets in tassel, number of ovules per ear, average length of styles, and number of days from planting to blooming.

At first glance it might be concluded that the characters of Euchlaena are, for the most part, dominant over those of the other two genera; but further study shows that the hybrid exhibits, in almost every case, the character which is common to two of the three parents. It so happens that every qualitative character of Euchlaena among those considered, except the presence of secondary branches in the tassel, also occurs in one of the other genera. Euchlaena resembles Zea in annual growth habit, absence of rhizomes, pedicels on the second male spikelet, bracts or husks enclosing the spike, and branching of lateral inflorescence. Euchlaena resembles Tripsacum in the absence of the central spike in the tassel, number of rows of functional pistillate spikelets, brittleness of the rachis, and an indurated shell consisting of the rachis and outer glume enclosing the seed. Thus in nine of the ten qualitative characters considered, Euchlaena resembles one of the other genera, as well as the hybrid. The tenth character, absence of secondary branches in the tassel, is common to Zea and Tripsacum but not to Euchlaena, and here the hybrid resembles the first two genera and not the last. All of the qualitative characters, then, exhibit the same kind of dominance relationships shown by flinty and floury endosperm in maize, where two doses of one are always dominant over a single dose of the other. The marked resemblance of the hybrid to Euchlaena may be nothing more than the expression of this type of inheritance.

Fig. 55. Variation in tassels. From left to right, Tripsacum, Zea X Tripsacum, (Zea X Tripsacum) X Euchlaena, Euchlaena, Zea. Note absence of central spike in all tassels except that of Zea.

Though two doses of one character are always dominant to one dose of the other, the dominance is by no means complete and the influence of the "recessive" parent is usually apparent in the hybrid. Though the hybrid, like Zea and Euchlaena, is an annual, it has a weak perennial tendency; the ears are enclosed in husks, but these are often too short to cover the entire spike; one of the male spikelets is pedicelled but the pedicel is much shorter than that of either pedicelled parent. And, though the hybrid resembles Euchlaena and Tripsacum in having a brittle rachis, it is one which disarticulates less readily than that of these two genera; the seed is enclosed in an indurated shell, but this structure is less horny than that of Tripsacum and Euchlaena. In fact, the only characters which exhibit a clear-cut dominance when two doses occur are the absence of root stocks and the absence of the central spike in the tassel.

When we consider the quantitative characters we see that they are inherited in precisely the same way except that the dominance of a condition received from two of the three parents is not quite so clear-cut. The hybrid resembles Euchlaena and Zea in having wide leaves, few nerves per unit of width, few pistillate spikelets in the tassel, and in having the bipartite style fused most of its length; it resembles Euchlaena and Tripsacum in having numerous tillers, many ears, few ovules per ear, and a long period from planting to blooming; it resembles Zea and Tripsacum in having a relatively small number of staminate florets. In these characters, as with the qualitative characters discussed previously, the influence of the third genus is usually apparent. The presence of pistillate spikelets in the tassel is a good example of this. Neither Zea nor Euchlaena normally has pistillate spikelets in the tassel, though in some genetic types this condition occurs regularly and it may also be induced in almost any variety by abnormal growing conditions. Tripsacum, on the other hand, always has pistillate spikelets in the terminal inflorescence. In our Tripsacum the ratio of staminate to pistillate spikelets is 15.2:1. Weatherwax (1918) reports a ratio of 18.5:1 in his stock. In the triple hybrid the ratio is 239:1.

In characters in which the three genera are all different, the condition in the hybrid approaches the average of the three parents. In length of styles, for example, the parents are 233 mm., 76 mm., and 14 mm., with an average of 108 mm. The average length of styles in the hybrid is 99 mm. When two of the parents are rather closely alike, however, the hybrid seems to approach the condition of the two similar parents more closely than it approaches the average of all three. Number of seeds per spike is a good example of this phenomenon. Euchlaena and Tripsacum are both low, with averages of 5.7 and 9.6 ovules, respectively. The variety of Zea used in this hybrid has an average of 485 ovules per spike. The average of the three parents is 167 ovules. The average of the hybrid is 14.2, which approaches Tripsacum and Euchlaena much more closely than it does the average of all three. The same situation holds for width of leaves, number of veins per cm., percentage of length that the styles are fused, percentage of pistillate spikelets in the tassel, and number of days from planting to blooming.

Cytology: Root tips from several plants showed 38 chromosomes, the expected number resulting from combining 10 from Zea, 18 from Tripsacum and 10 from Euchlaena (Fig. 56A).

The behavior of the chromosomes throughout meiosis was so similar to that described in the triploid hybrid (Zea x Tripsacum) x Zea that the description already given for the latter (p. 111) applies almost equally well to this one.

The Zea and Euchlaena chromosomes paired in a fairly regular manner (Fig. 56B) and the other 18 chromosomes lagged, except when a few trisomes occurred. Theoretically, the pairing of the 10 bivalent chromosomes should not be quite so regular as in the backcross by Zea, because in ordinary hybrids between Zea and Euchlaena slight irregularities occur, as reported by several investigators (see page 49). But if the irregularities of chromosome behavior are greater in this triple hybrid than in the backcross, the differences are slight. We can conclude from these observations that the chromosomes of Euchlaena are much more closely related to those of Zea than to those of Tripsacum. If there is any affinity of Euchlaena chromosomes for those of Tripsacum, it is completely overshadowed by the much greater affinity between Zea and Euchlaena chromosomes.

Fig. 56. Chromosomes of trigeneric hybrid of Zea, Euchlaena, and Tripsacum; X 2550. A. Root-tip cell; 38 chromosomes. B. Division-I figure, showing 10 ZE chromosome in metaphase condition and 18 T chromosomes lagging.

The Progeny of the Triploid Hybrid (Zea x Tripsacum 2n) x Zea

The 374 seeds resulting from pollinating, with maize pollen, 1758 silks of the triploid hybrid ZZT were started in a germinator, transplanted to pots in the greenhouse, and finally moved to the field. Unfortunately no records were kept on percentage of germination, so we have no data on seedling mortality. Our records show, however, that 211 plants were moved to the field and of this number 178 finally reached maturity. This number constitutes but 10.1 per cent of the 1758 pollinations which had been made, and it is evident that there has been an elimination of practically nine-tenths of the gametes produced by the triploid hybrid. Most of this elimination was functional, for the silks of the triploid hybrid were pollinated again and again to insure that none escaped, and every precaution was taken to keep alive all plants which were capable of surviving.

Since there had been fairly regular pairing of the 20 maize chromosomes in the parental triploid hybrid, followed by regular separation of the members of each pair, and since the 18 unpaired Tripsacum chromosomes had assorted more or less at random, we anticipated that this population of plants would be an extremely variable one. All plants, however, were expected to possess 20 Zea chromosomes and to differ primarily in the number of extra Tripsacum chromosomes which had been superimposed upon the normal Zea chromosome complex. The number of extra Tripsacum chromosomes might theoretically vary between 0 and 18 and if the population were large enough we should expect to find variation extending from normal corn plants, on the one hand, to plants duplicating the parental triploid hybrid on the other. In what proportions these two extremes and their various intermediates would occur, we had no way of anticipating, for it was reasonably certain that the population would be the product of two opposing forces. Random assortment of the unpaired Tripsacum chromosomes would tend to produce a majority of gametes with an intermediate number of Tripsacum chromosomes; but selective elimination would favor those with few Tripsacum chromosomes approaching the balanced condition of the Zea parent, or those with many Tripsacum chromosomes approaching the balanced condition of the parental triploid.

We had planned to determine the chromosome number of each plant at meiosis and hence had decided to make no root tip preparations. When the plants began to approach the flowering stage we found it impossible, however, to examine the chromosomes of each plant immediately when the proper stage was reached, and were compelled, instead, to make collections of material to be stored for examination later. This procedure proved to be decidedly unsatisfactory, for not only did much of the material deteriorate in storage so that accurate chromosome counts were difficult to make; but much of it proved to be at the wrong stage, so that in the end accurate counts were available for only a relatively small number of plants. Even more unfortunate, however, was the fact that the plants which were most Tripsacum-like, presumably those with the largest number of Tripsacum chromosomes, involved the greatest errors in judgment in the collection of material for cytological examination, so that chromosome counts from these plants were rarely obtained.

We should, therefore, have had but a very meager picture of the cytological conditions in this population had we not encountered a phenomenon which permitted us to estimate the chromosome number of each plant, with what appears to be a high degree of accuracy, especially in plants where the number was relatively small.

In order to determine the relationship between the number of Tripsacum chromosomes and the percentage of empty pollen, we had made pollen or anther collections from every plant in the population. The pollen from both Zea and Tripsacum desiccates and shrivels soon after dehiscence, but can be restored to its original size and shape by mounting in lactic acid. The addition of a few crystals of iodine to the acid results in a deep staining of the contents of the grains and permits a ready distinction to be made between sound and empty grains.

When we began to examine the pollen from plants in which the chromosome number had been determined, we found immediately that plants with one extra Tripsacum chromosome, though maturing few empty pollen grains, produced pollen grains of two sizes, one size identical with normal maize pollen, the other smaller. In some plants the two types were so distinct that they could be counted separately and such counts always approached a 1:1 ratio. When two extra Tripsacum chromosomes were present the plants produced three classes of pollen. Approximately one-fourth of the grains were normal and well filled; approximately half were small, but sound or partially filled; the remaining fourth were empty.

These observations led to the conclusion that one extra Tripsacum chromosome reduces the size of the pollen grains, while two Tripsacum chromosomes result in empty pollen grains. If this is always true, it should be possible to determine the number of Tripsacum chromosomes which a plant in this population possesses, by counting the various types of pollen grains and determining the percentage of empty pollen. The theoretical percentage of empty pollen for plants with different numbers of Tripsacum chromosomes may be computed from the following formula, in which N is the number of Tripsacum chromosomes:

$$\text{Percentage of empty pollen} = \frac{2^N - (N + 1)}{2^N} \times 100.$$

The theoretical percentages of empty pollen resulting from various numbers of extra Tripsacum chromosomes ranging from 0 to 18 are shown in Table 9.

It is evident that when the number of extra Tripsacum chromosomes is more than 9, the differences between the percentages of empty pollen for different chromosome numbers is so slight that distinction between the groups is impossible. But with numbers below 9, and especially with numbers up to 3, there should be little difficulty in determining to which group a given plant belongs (Fig. 57).

The results of these pollen counts are tabulated in Tables 10-15, in which the plants are grouped into different classes with regard to the percentage of empty pollen which they produced. It is obvious that in

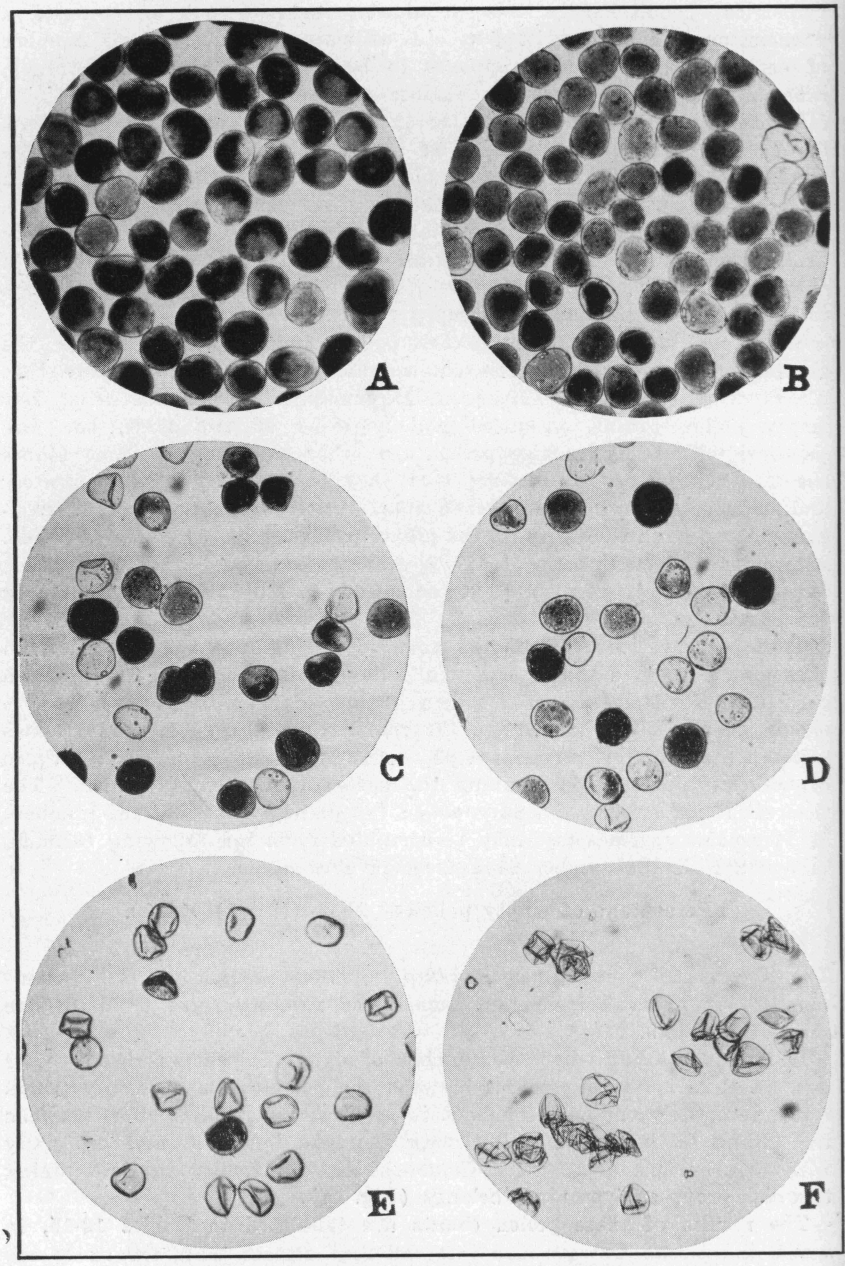

Fig. 57. Pollen from plants with differing numbers of Tripsacum chromosomes. A. Normal pollen from 2n plant. B. Variable pollen from 2n+1 plant. C. Pollen from 2n+2 plant. Approximately half of the pollen grains are small; one-fourth are empty. D. Pollen from 2n+3 plant; 50 per cent empty. E. Pollen from 2n+9 plant; 98 per cent empty. F. Pollen from 2n+18 plant; 100 per cent empty.

most cases there is no question as to which group a given plant belongs. There are exceptions to almost all rules, however. Plant No. 10-40 (Table 12), for example, produced 44.9 per cent of empty pollen and if no further data were available, would be included in the group with three extra chromosomes. It happens, however, that the remaining 55.1 per cent of the grains are normal; whereas, if three chromosomes were involved, only one-fourth of them should have been normal, the other three-fourths reduced in size. There is always some variation in the reduced grains in any plant, ranging from those which are almost normal in size to those which are empty. Thus plants with one extra chromosome almost always have a slightly higher percentage of empty grains than those with none. In the case of Plant No. 10-40, nearly all of the reduced grains were empty.

Table 9. Theoretical percentages of empty pollen in plants with various numbers of Tripsacum chromosomes

No. Tripsacum chromosomes	Per cent empty pollen	No. Tripsacum chromosomes	Per cent empty pollen
0	0	10	98.926
1	0	11	99.414
2	25.000	12	99.683
3	50.000	13	99.829
4	68.750	14	99.908
5	81.250	15	99.951
6	89.063	16	99.974
7	93.750	17	99.986
8	96.484	18	99.993
9	98.047		

Table 10. Pollen segregation in plants classified as having normal pollen (no Tripsacum chromosomes)

Plant No.	Total grains examined	Empty	
		No.	Per cent
8–4	225	0	0
8–6	140	1	.7
8–19	94	4	4.3
8–27	319	2	.6
8–29	274	3	1.1
8–42	66	6	9.1
10–8	139	2	1.4
10–27	143	0	0
11–10	205	7	3.4
11–12	302	3	1.0
11–27	172	0	0
11–32	88	1	1.1
11–34	255	1	.4
11–37	205	2	1.0
11–42	237	4	1.7
12–18	201	4	2.0
12–19	119	9	7.6
12–31	222	1	.5
12–32	219	10	4.6
12–33	186	1	.5
12–35	222	14	6.3
12–39	246	1	.4
12–42	195	13	6.7
12–44	208	2	1.0
12–46	202	1	.5
Total and average	4884	92	1.9

In the group with two extra chromosomes, on the other hand, there are six plants with percentages of empty pollen much below 25 per cent. Those are Nos. 9-9, 9-34, 10-28, 10-34, 10-37, and 12-12. All of these plants would have been regarded as having only one extra chromosome were it not for the fact that the percentage of normal pollen in each case approaches 25. All of these plants are included in the 2-chromosome group, but the exceptional percentages of empty pollen are omitted from the averages.

With these omissions the average percentages of empty pollen in the different groups approach with remarkable closeness the theoretical percentages shown in Table 9. This is illustrated in Fig. 58 in which the theoretical percentages are represented by the curve and the actual percentages by points.

Table 11. Pollen segregation in plants classified as having slightly variable pollen (1 Tripsacum chromosome)

Plant No.	Total grains examined	Empty	
		No.	Per cent
8–8	107	5	4.7
8–25	215	6	2.8
8–26	408	6	1.5
8–32	117	4	3.4
8–34	144	6	4.2
8–44	46	1	2.2
9–3	178	7	3.9
9–4	253	18	7.1
9–6	169	2	1.2
9–7	145	3	2.1
9–23	181	3	1.7
9–35	170	6	3.5
10–5	130	8	6.2
10–12	223	4	1.8
10–19	430	16	3.7
10–23	167	5	3.0
10–26	152	6	4.0
10–30	248	7	2.8
10–33	168	9	5.4
10–42	83	2	2.4
10–43	199	15	7.5
11–6	167	3	1.8
11–7	214	25	11.7
11–15	179	6	3.4
11–18	162	1	.6
11–22	253	7	2.8
11–26	242	20	8.3
11–28	268	48	17.9
11–40	139	8	5.8
12–10	277	19	6.9
12–11	264	19	7.2
12–22	126	6	4.8
12–24	210	14	6.7
12–29	236	10	4.2
Total and average	6670	325	4.9

It is obvious, we believe, that the actual results could be fitted into this theoretical scheme with such a remarkably close agreement, only if the theoretical scheme is a sound one. It is true that the averages which we have obtained by grouping the plants in this way are compelled to show some relation to the theoretical averages because the plants were grouped according to the theoretical averages. This may appear to be reasoning in a circle and to a certain extent it is. On the other hand, the grouping is not based on percentage of empty pollen alone. For example, plants 9-40 and 10-16 with 75.8 and 75.6 per cent respectively of empty pollen are closer to the 2n + 5 group with 81.3 per cent of empty pollen than to the 2n + 4 group with 68.8 per cent of empty pollen. Yet the percentage of small sound grains indicates that these two plants are 2n + 4. Plant No. 11-30 on the other hand with 76.1 per cent of empty pollen shows a percentage of small pollen which put its into the 2n + 5 class.

Table 12. Pollen segregation in plants classified as having highly variable pollen (1 Tripsacum chromosome) in which normal and reduced grains were not readily distinguishable

Plant No.	Total grains examined	Empty	
		No.	Per cent
8–5	257	12	4.7
8–11	77	8	10.4
8–15	191	16	8.4
8–18	110	1	.9
8–37	228	13	5.7
9–29	112	3	2.7
9–30	130	5	3.9
9–44	123	11	8.9
10–11	114	13	11.4
10–13	206	28	13.6
10–14	166	8	4.8
10–15	169	7	4.1
10–18	206	13	6.3
10–29	191	15	7.9
10–31	177	12	6.8
10–38	196	25	12.8
10–40	194	87	44.9*
11–2	110	8	7.3
11–3	185	16	8.6
11–5	125	8	6.4
11–13	159	7	4.4
11–23	153	26	17.0
11–33	209	1	.5
11–44	226	6	2.7
12–20	192	8	4.2
12–26	273	15	5.5
12–28	285	17	6.0
12–34	130	4	3.1
12–36	214	16	7.5
12–38	102	3	2.9
Total and average	5016	325	6.5

*Omitted from average.

The facts that (1) the majority of the percentages fall so precisely into one or another of the theoretical groups, especially in cases where a small number of Tripsacum chromosomes is involved; (2) the percentages of small pollen are also in agreement with the theoretical percentages; and (3) the averages obtained by grouping the plants agrees so closely with the theoretical averages, have convinced us that a determination of the percentage of empty pollen is a sound basis for estimating the number of extra Tripsacum chromosomes involved. We use the word "estimate" in the sense which chemists use it to distinguish results

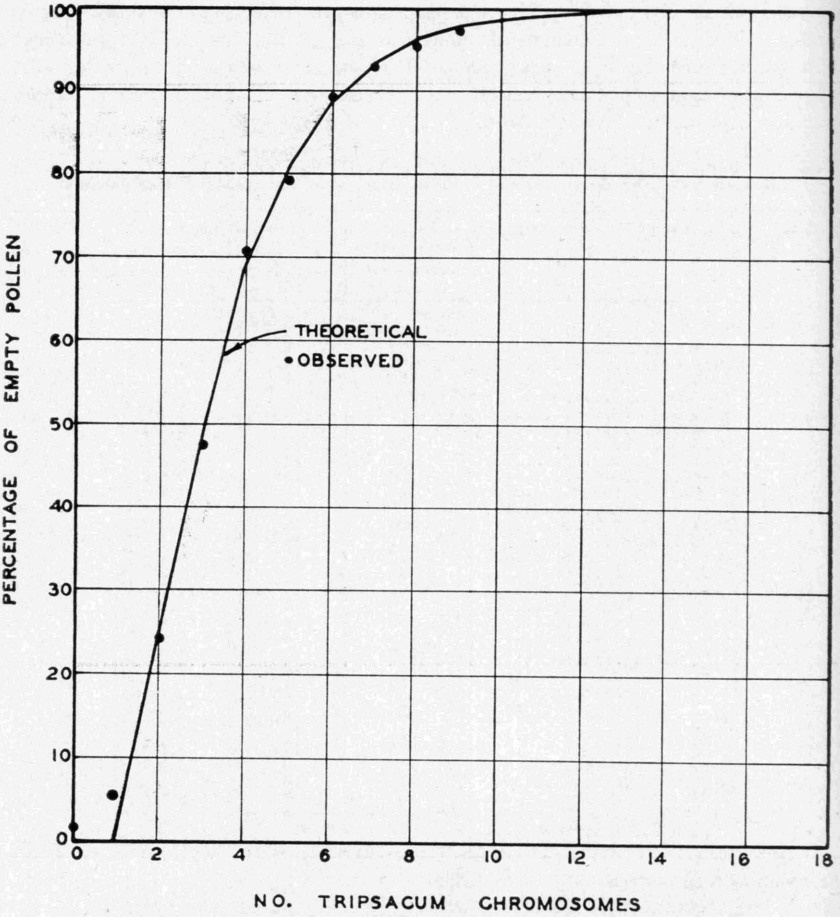

Fig. 58. Theoretical and observed percentages of empty pollen in segregates from the triploid hybrid (Zea X Tripsacum) X Zea.

obtained by indirect methods from those resulting from actual analyses, and not in the sense that the results are necessarily less accurate.

On the basis of estimated chromosome numbers the 178 plants in this population fall into the following classes:

No. Tripsacum Chromosomes	No. Plants
0	25
1	76
2	22
3	4
4	8
5	3
6	3
7	4
8	6
9	5
10 or more	22

Table 13. **Pollen segregation in plants classified as having highly variable pollen (1 Tripsacum chromosome) in which normal and reduced grains were distinguishable**

Plant No.	Total grains examined	No.			Per cent		
		Normal	Reduced	Empty	Normal	Reduced	Empty
8–9	141	70	67	4	49.6	47.5	2.8
8–17	172	113	32	27	65.7	18.6	15.7
8–21	267	125	140	2	46.8	52.4	.7
8–31	165	76	83	6	46.1	50.3	3.6
9–5	217	112	103	2	51.6	47.5	.9
10–20	216	95	119	2	44.0	55.1	.9
10–41	217	82	125	10	37.8	57.6	4.6
11–8	312	175	131	6	56.1	42.0	1.9
11–36	334	136	178	10	42.0	54.9	3.1
11–43	226	103	76	47	45.6	33.6	20.8
12–23	216	90	110	16	41.7	50.9	7.4
12–45	221	90	105	26	40.7	47.5	11.8
Total and average	2694	1267	1269	158	47.0	47.1	5.9

It is evident at once that the first three groups with 0, 1, and 2 Tripsacum chromosomes respectively, are entirely too large to be the result of random assortment of the 18 Tripsacum chromosomes, for even with the 90 per cent of gametic and other elimination which has occurred, there is no possibility of such a high proportion of these combinations occurring as the result of random assortment. Expansion of the binomial $(\frac{1}{2} + \frac{1}{2})^{18}$ reveals that, with random assortment, only one gamete in 262,144 should receive no Tripsacium chromosome, 18 should receive one, and 153 should receive two. Thus with random assortment only one gamete in 1524 should be found in these three groups. Yet from 1758 gametes, 123 plants or approximately 1 in 14 are in this category. Obviously we are dealing with a segregation which does not involve completely random assortment, a conclusion further substantiated by the fact that we do not find a similar excess of plants with 16, 17, and 18 chromosomes, which represent the corresponding combinations at the other end of the binomial distribution. We cannot, of course, determine the chromosome number by pollen examination when it becomes higher than 9, but the entire group of plants with numbers above 9 comprises only 22.

Table 14. Pollen segregation in plants classified as having approximately 25 per cent of empty pollen (2 Tripsacum chromosomes)

Plant No.	Total grains examined	No.			Per cent		
		Normal	Reduced	Empty	Normal	Reduced	Empty
8–10	310	54	184	72	17.4	59.4	23.2
8–12	236	73	108	55	30.9	45.8	23.3
8–22	227	40	122	65	17.6	53.7	28.6
8–28	225	64	108	53	28.4	58.0	23.6
8–36	222	65	98	59	29.3	44.1	26.6
8–38	139	....	....	46	....	....	33.1
8–41	294	....	....	73	....	....	24.8
8–43	421	....	....	89	....	....	21.1
9–9	389	119	247	23	30.6	63.5	5.9*
9–11	187	55	85	47	29.4	45.5	25.1
9–16	232	53	117	62	22.8	50.4	26.7
9–34	129	46	68	15	35.7	52.7	11.6*
10–21	166	....	....	47	....	....	28.3
10–22	264	47	155	62	17.8	58.7	23.5
10–28	233	61	153	19	26.2	65.7	8.2*
10–34	208	56	146	6	26.9	70.2	2.9*
10–37	199	51	106	42	25.6	53.3	21.1
11–1	178	43	116	19	24.2	65.2	10.7*
11–11	312	....	....	57	....	....	18.3
11–14	222	56	111	55	25.2	50.0	24.8
12–12	141	42	78	21	29.8	55.3	14.9*
12–30	178	48	77	53	27.0	43.3	29.8
Total and av.	5112	....	....	1040	....	....	20.3
Total and av.*	3834	....	....	937	....	....	24.4
Total and av.	3780	973	2079	728	25.7	55.0	19.3

*Omitted from this average.

The preponderance of plants with a low chromosome number becomes explicable when we re-examine the description and illustrations of cytological behavior in the parental triploid hybrid (p. 111). It will be recalled that in most cells one or several trivalents were found which were interpreted as the result of a feeble union of a Tripsacum chromosome with a pair of Zea chromosomes. It will be recalled also, and the observation is illustrated in Figure 46B, that numerous micronuclei were formed presumably from the lagging Tripsacum chromosomes. This phenomenon is accompanied by quartets of an entirely irregular structure which are much more common than the regular type.

Apparently, then, the population of 178 plants represents two distinct distributions superimposed upon each other—one in which a few Tripsacum chromosomes associate with the Zea chromosomes and assort at random with them, while all other Tripsacum chromosomes are excluded by the production of micronuclei; the other in which the non-paired Tripsacum chromosomes assort at random.

Table 15. Pollen segregation in plants classified as having 50—99 + per cent of empty pollen (3—10 + Tripsacum chromosomes)

Plant No.	Total grains examined	Empty	
		No.	Per cent
	Approximately 50% empty		
8-35	128	55	43.0
9-41	191	106	55.5
9-42	175	98	56.0
12-40	245	95	38.8 (1)
Total and average	739	354	47.9
	Approximately 68.8% empty		
8-40	310	212	68.4
9-13	219	147	67.1
9-19	378	272	72.0
9-33	284	205	72.2
9-40	186	141	75.8 (2)
10-6	207	152	73.4 (3)
10-16	201	152	75.6 (4)
11-41	232	152	65.5
Total and average	2017	1433	71.0
	Approximately 81.3% empty		
10-44	225	189	84.0
11-30	230	175	76.1 (5)
12-41	265	210	79.2
Total and average	720	574	79.7
	Approximately 89.1% empty		
8-39	231	199	86.2
11-16	204	185	90.7
12-15	291	264	91.8
Total and average	726	648	89.3
	Approximately 93.8% empty		
8-14	231	214	92.6
9-24	178	166	93.3
9-26	337	314	93.2
11-19	264	248	93.9
Total and average	1010	942	93.3
	Approximately 96.5% empty		
9-14	156	148	96.9
9-21	211	204	96.7
9-25	407	388	95.3
10-10	315	302	95.9
11-38	296	284	95.9
11-39	220	212	96.4
Total and average	1605	1538	95.8
	Approximately 98.0% empty		
10-32	217	214	98.6
11-9	286	279	97.6
11-35	274	269	98.2
12-25	375	367	97.9
12-27	297	289	97.3
Total and average	1449	1418	97.9

Table 15. Pollen segregation in plants classified as having 50—99+ per cent of empty pollen (3—10+ Tripsacum chromosomes)—Continued

Plant No.	Total grains examined	Empty	
		No.	Per cent
	More than 99% empty		
8–13	451	447	99.1
8–33	2500 +	2500 +	100.0
9–1	1000 +	1000 +	100.0
9–8	2000 +	2000 +	100.0
9–10	5000 +	5000 +	100.0
9–12	4000 +	4000 +	99.9 +(6)
9–15	300 +	300 +	100.0
9–20	2000 +	2000 +	100.0
9–22	241	240	99.6
9–31	3000 +	3000 +	100.0
9–37	1000 +	1000 +	100.0
9–43	1000 +	1000 +	100.0
10–3	1000 +	1000 +	100.0
10–17	1000 +	1000 +	100.0
10–36	1000 +	1000 +	100.0
11–17	1000 +	1000 +	100.0
11–20	1000 +	1000 +	100.0
11–21	1000 +	1000 +	100.0
11–29	1000 +	1000 +	100.0
12–16	2000 +	2000 +	100.0
12–21	3000 +	3000 +	100.0
12–37	1000 +	1000 +	100.0
Average approximately			99.9 +

(1) Plant No. 12-40 had 14.3 per cent of normal pollen; 12.5 per cent expected with 3 Tripsacum chromosomes.

(2) Plant No. 9-40 had 7.5 per cent of normal pollen; 6.3 per cent expected with 4 Tripsacum chromosomes.

(3) Plant No. 10-6 had 5.3 per cent of normal pollen; 6.3 per cent expected with 4 Tripsacum chromosomes.

(4) Plant No. 10-16 had 7.3 per cent of normal pollen; 6.3 per cent expected with 4 Tripsacum chromosomes.

(5) Plant No. 11-30 had 2.7 per cent of normal pollen; 3.1 per cent expected with 5 Tripsacum chromosomes.

(6) Plant No. 9-12 had 4 small sound grains in a sample of approximately 4000 grains.

How many Tripsacum chromosomes there are that regularly form trivalents with the paired Zea chromosomes is impossible to determine. One trisome was nearly always observed, but the number sometimes appeared to be as high as four (Fig. 45D).

The distribution of plants with Tripsacum chromosome numbers of 0, 1, and 2 in the succeeding generation, however, suggests that the average number is approximately two; for if two Tripsacum chromosomes paired regularly with the Zea chromosomes and assorted at random to one pole or the other, we should have a distribution of 1:2:1 for the gametes carrying 0, 1, and 2 chromosomes respectively. The distribution which actually occurred 25:76:22 does not differ significantly ($P = .05$) from a 1:2:1 ratio.

If these results are the consequence of a regular association of two Tripsacum chromosomes with the paired Zea chromosomes, it is very likely that it is always the same two Tripsacum chromosomes which are involved. In this case the 76 plants with one extra chromosome should comprise two distinct classes with regard to which of the two extra

Tripsacum chromosomes is present, while all the plants in the class with two extra chromosomes should be identical in possessing both of these particular chromosomes. Unfortunately, this possibility did not occur until after the chromosome numbers had been determined, which was long after the plants had matured and died; so that it was not possible to attempt a classification among the plants in the field. Pollen had, however, been saved from every plant, as well as one branch of the tassel bearing male spikelets. Examination of the pollen showed that there were two distinct types of reduced pollen, one of which differed from normal pollen only in being slightly smaller and another which differed more markedly in size and also in the fact that the contents of the pollen grain sometimes stained more darkly with iodine than the contents of nomal grains. These two types of reduced pollen occurred in approximately equal numbers in the 76 plants which had been classified as possessing one Tripsacum chromosome. Microscopic examination of the glumes of the staminate spikelets from these 76 plants also showed two fairly distinct types—one in which the glumes did not differ essentially from those of normal maize and another in which a decided Tripsacum influence was apparent in the reduction of long hairs on the glumes, usually accompanied by an increase in the number of nerves. Classification of the plants into these two types also resulted in approximately a 1:1 ratio. When these two independent classifications — one on the basis of pollen, the other on glumes — were brought together, it was found that there was a decided correlation between the two, the plants with slightly reduced pollen nearly always showing no Tripsacum influence on the glumes and those with markedly reduced pollen exhibiting in most cases a decided Tripsacum influence. Where the two observations were not in agreement, it was frequently possible, upon re-examination, to change the classification in one characteristic or the other, for the distinction between the types either in pollen or glumes is not always clear-cut and there are many borderline cases which can be thrown into either class. But even with this procedure, which may indeed be an unwarranted attempt to fit the data into a preconceived scheme, there are still a few exceptions in which the glumes are definitely of one type, the pollen definitely of another. This may possibly be the result of a partial overlapping of the two types of pollen, the type with slightly reduced grains occasionally having markedly reduced grains and *vice versa;* it may be due to the occasional inclusion of a Tripsacum chromosome which is different from the two which appear most frequently; or it may be the result of a segmental interchange between a Zea and Tripsacum chromosome. There is some evidence for this in the plants with two extra chromosomes. If the same two completely Tripsacum chromosomes are always involved in the plants of this group, all should be identical in their glume characteristics. Of the 22 plants in this group, 20 are identical in having glumes which exhibit a marked Tripsacum effect; but the remaining two are different, showing a very slight or no Tripsacum effect upon the glumes.

There is some evidence, therefore, that the three groups of plants involving 0, 1, and 2 Tripsacum chromosomes are not entirely the result of the random assortment of two particular chromosomes; that one or more other Tripsacum chromosomes are occasionally involved. The frequency with which other chromosomes are included, however, cannot be large; for of the 22 plants with two Tripsacum chromosomes, 20 are identical in the characteristics of the glumes of the staminate spikelets.

Our final conclusion, therefore, is that the progeny of the triploid hybrid consists of two rather distinct groups of plants. The first results from gametes from which most of the Tripsacum chromatin has been excluded by the formation of supernumerary micronuclei, and in which several Tripsacum chromosomes, usually two, which associate more or less regularly with those of Zea, are distributed at random. The second group is superimposed upon the first and the remaining 16 Tripsacum chromosomes are not excluded from the gametes but assort at random. Under these conditions we should expect a rather large number of plants with no Tripsacum chromosomes, and we actually obtained 22. We should expect none which possess all 18 Tripsacum chromosomes in a population of this size, and none occurred which duplicated the parental triploid. There was one plant which in its general appearance and in a number of characteristics was much more like Tripsacum than the triploid parent, but in other characteristics it did not approach Tripsacum as closely as the triploid. This condition becomes explicable when the effect of different numbers of Tripsacum chromosomes upon the characteristics which distinguish Zea and Tripsacum are considered in succeeding pages.

There remains only one discrepancy in the picture—the percentage of empty pollen in the parental triploid. From 1758 pollinated ovules we obtained 25 plants with no Tripsacum chromosomes and 76 with one Tripsacum chromosome. This indicates that in the parental triploid one pollen grain in 70 should have been normal; one in 23 reduced but sound. We have examined thousands of pollen grains from the triploid hybrid without discovering a single normal or reduced grain; all are empty. This situation is similar to that found in the diploid hybrid Zea x Tripsacum (2n) where sound pollen grains might have been expected to develop from the unreduced gametes, but where none were found. We have already suggested (p. 109) several possible interpretations of this.

The Relation of Number of Tripsacum Chromosomes to Morphological Characteristics of the Plants

It became apparent almost immediately when cytological studies of the plants in the segregating generation were begun that there was a decided correlation between the number of extra Tripsacum chromosomes and the characteristics of the plants (Figs. 59-60). Those with no Tripsacum chromosomes were, for the most part, normal corn plants differing in no way from ordinary corn plants, although half of their parentage was contributed by Zea chromosomes from the triploid hybrid. No better example than this of the marvelous individuality of the chromosomes could be found, for after occupying the same nuclei with Tripsacum chromosomes for two plant generations and untold cell generations, most of the Zea chromosomes segregated out intact and completely uncontaminated by their association with those of Tripsacum. A few plants were found, it is true, which possessed no Tripsacum chromosomes but which exhibited a perceptible trace of Tripsacum influence; but these were the exception rather than the rule.

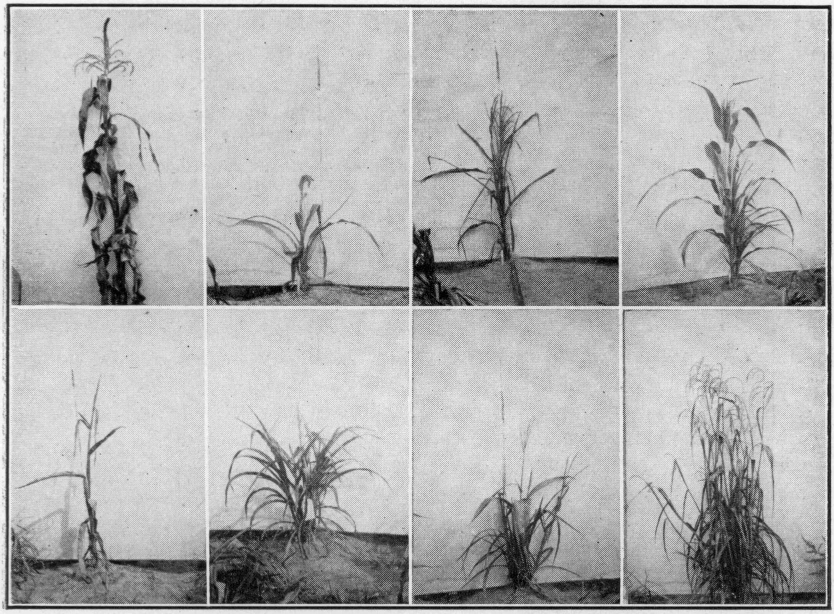

Fig. 59. **Segregates from the cross [(Zea X Tripsacum) X Zea] X Zea. All of these plants possess 20 Zea chromosomes and extra Tripsacum chromosomes as follows: upper row, 0, 1, 2, 6; lower row, 8, 10+, 10+, 13+.**

Plants with Tripsacum chromosomes, however, all showed some Tripsacum influence and in general there was a decided correlation between the number of Tripsacum chromosomes and the degree of Tripsacum influence which was exhibited. It was apparent, however, that the individual characteristics were the product of two forces which sometimes opposed each other, sometimes operated in the same direction. These forces are (1) the concentration of Tripsacum genes, an increase in number of Tripsacum genes tending to bring about deviations away from the Zea type and toward the Tripsacum type; and (2) chromosomal unbalance, which tends to reduce vigor and thus has an effect upon the expression of a number of characteristics in which the two genera

Fig. 60. Lateral inflorescence of the most Tripsacum-like segregate from a Zea-Tripsacum cross. (Fig. 59). Except for the absence of the staminate portion of the inflorescence which has been accidentally lost, this spike is almost an exact duplicate of that of the parental triploid hybrid (Zea X Tripsacum) X Zea (see Fig. 44).

differ. In order to determine the relationship of the extra Tripsacum chromosomes to various other characteristics a number of measurements and observations were made as follows:

1. Days to silking. The difference in number of days between planting and the first appearance of silks. In Texas, corn planted on March 1 usually silks late in May, or early in June, Tripsacum not until fall and sometimes not until the following spring. Data on this character were obtained from 159 of the 178 plants.
2. Height of stalk. The height of the main stalk measured in centimeters from the ground to the base of the tassel. Most varieties

of corn are considerably taller than the plants of the diploid *T. dactyloides*. The addition of Tripsacum chromosomes would be expected to reduce height of stalk. Data on this characteristic were recorded for all plants.

3. Number of tillers. Actual count. Corn tillers sparingly; Tripsacum profusely. Data obtained from all plants.
4. Number of leaves. Actual count of leaves on main stalk and tillers. Tripsacum has many times the number of leaves of Zea, partly by virtue of its profuse tillering. Data obtained from all plants.
5. Number of ears. Actual count of the lateral inflorescences from which silks emerged. Zea usually has few; Tripsacum many. A state of chromosomal unbalance suppresses ear formation and hence many of the plants in this population produced no ears. These are recorded as zero, and included in the average.
6. Number of tassel branches. Actual count of all branches except the central spike. The tassel of maize branches profusely; the terminal inflorescence of *T. dactyloides* seldom has more than five branches. Data available on all plants but one.
7. Number of male spikelets. An estimate arrived at by counting the number of spikelets on a typical branch and multiplying by the number of branches. Hence the total number of male spikelets is closely related to the number of tassel branches, but not wholly dependent upon it. Maize has numerous spikelets in the terminal inflorescence; Tripsacum a much smaller number. Data available from all plants but one.
8. Leaf index. Length divided by width. Length was measured on the leaf arising from the upper ear-bearing node, width on the widest part of the same leaf. The leaf index of Zea is low; of Tripsacum very high. Data available for all plants, for though some produced no ears from which silks emerged, practically all produced ear shoots. In the remainder the leaf to be measured was arbitrarily chosen.
9. Venation index. The number of veins on the same leaf as above divided by the width. Zea has a low number of leaf veins per unit of width; Tripsacum a high number. This character is but little influenced by environment and presumably also but little by a chromosomal unbalance. It is one of the best measures of the effect of a concentration of Tripsacum genes.
10. Number of rows of pistillate spikelets. The pistillate spikelets of the ears of Zea are usually paired, and the number of rows of spikelets is therefore half that of the number of rows of grain, and ordinarily varies from four to ten. In Tripsacum the spikelets are single and two-rowed. Data available from 131 plants.
11. Per cent fertility. An estimate arrived at by counting the ovules on the pollinated portion of the ear and multiplying by the number of rows. Since time did not permit repeated pollinations of the same ear, some of the failures to produce seed are the result of incomplete

pollination rather than non-functioning of the ovules. All plants were treated alike in this respect, however, so that the data are comparable, within the limits of sampling error. This measurement has no bearing on the differences between Zea and Tripsacum, for both are fully fertile when self-pollinated. Data are available from 102 plants.

12. Total ovules per ear. An estimate arrived at by counting the ovules on one row and multiplying by the number of rows. Zea usually bears several hundred or more ovules per ear. Data available from only 86 plants, which are probably not a random sample of the population; for the less vigorous plants, resulting from chromosome unbalance, are those most likely to have had no ears.
13. Percentage of empty pollen. Determined as previously described by actual count under microscopic examination. Data available from all plants.

The averages for these different classes of plants are set forth in Table 16 and Fig. 61. No constants to measure the variation or error have been computed, for in some cases the individual populations are so small that the constants would obviously have been meaningless. We must depend, therefore, upon the consistency with which the results point to certain conclusions, rather than upon statistical significance of differences between groups.

It requires no more than a glance at the data to show that in most characteristics there is a trend from the condition of Zea to that of Tripsacum with an increase in the estimated number of Tripsacum chromosomes. This trend is to some extent obscured by the marked fluctuations in the averages which have presumably resulted from sampling errors. In order to reduce the sampling errors to a minimum, we have combined the population into five large-sized groups — the first comprising the 25 plants with no extra chromosomes; the second, the two types of plants with one extra chromosome; the third, the plants with two extra chromosomes; the fourth, all plants with extra chromosomes ranging from three to nine in number; and the fifth, all plants with more than nine extra chromosomes. The two last named groups demand additional explanation. We have designated the fourth group as having an average of six Tripsacum chromosomes. This is the median number and it also proves to be almost the weighted average, which is actually 5.97. The last group of 22 plants is designated as having an average chromosome number of 13. Since we have no data on the chromosome numbers in plants which possess more than nine, the designation is purely an arbitrary one. It is, however, based on the assumption, a valid one, we believe, that the distribution of chromosome numbers from 10 to 16 would be expected to follow the same pattern as that from 3 to 9. With random distribution of the chromosomes, the number 16 for example, is just as likely to occur as the number 3, and both represent the same departure from a balanced condition.

The averages of the five groups so arranged are set forth in Table 16, and shown graphically in Fig. 62.

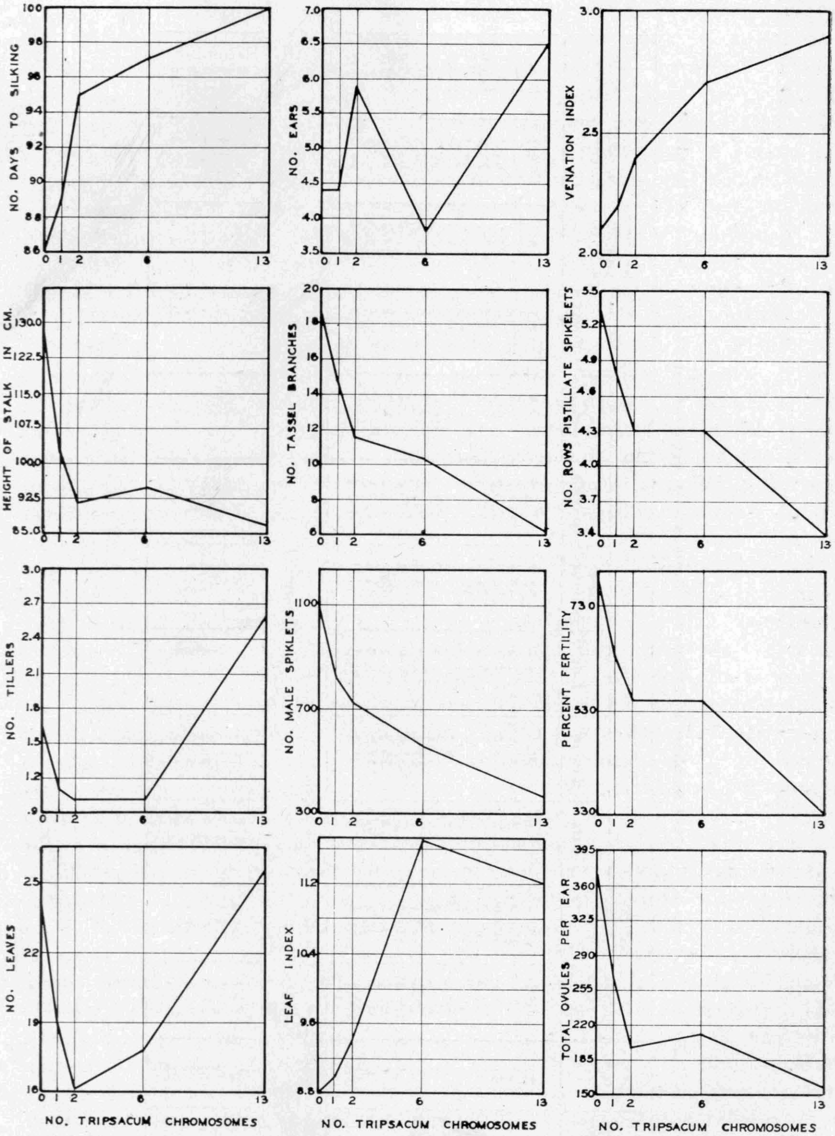

Fig. 61. **Relation between number of Tripsacum chromosomes and the expression of various quantitative characteristics by which Zea and Tripsacum differ.**

Table 16. Effects of different numbers of Tripsacum chromosomes upon various characteristics of the plants

No. Tripsacum chromosomes	No. of plants	No. days to silks	Height of stalk, cm.	No.					Index		No. rows pistillate spikelets	Per cent fertility	Total ovules	Per cent empty pollen
				Tillers	Leaves	Ears	Tassel branches	Male spikelets	Leaf	Venation				
0..........	25	86.4	128.9	1.6	24.4	4.4	18.7	1116.4	8.8	2.1	5.4	78.2	376.9	1.9
1*..........	34	90.3	103.2	1.1	17.9	4.2	15.6	871.9	8.9	2.3	5.0	63.3	269.6	4.9
1**........	42	88.2	100.6	1.2	19.6	4.5	14.0	790.9	9.1	2.2	4.6	63.4	250.4	6.3
2..........	22	95.0	91.7	1.0	16.2	5.9	11.5	726.0	9.4	2.4	4.3	55.0	195.0	24.4
3..........	4	91.7	102.8	1.5	22.0	4.0	19.0	1073.5	13.2	2.8	4.7	54.1	218.7	47.9
4..........	8	96.5	95.8	.4	12.3	3.5	10.4	591.3	14.1	3.0	4.6	75.9	250.0	71.0
5..........	3	91.0	78.0	.7	11.7	2.7	4.7	173.0	14.9	2.9	4.0	58.0	....	79.7
6..........	3	99.3	96.1	.7	11.7	2.0	4.0	311.0	12.2	3.0	4.0	76.3	256.0	89.3
7..........	4	102.3	110.5	3.3	37.0	9.8	8.8	370.5	9.7	2.6	2.0	50.0	34.0	93.3
8..........	6	96.6	91.0	.5	15.8	3.1	10.1	475.3	8.2	2.2	4.3	27.9	240.0	95.8
9..........	5	98.7	86.2	.8	17.2	2.0	11.8	732.8	10.2	2.4	4.5	30.3	....	97.9
10–16 (13).....	22	100.1	86.6	2.6	25.6	6.5	6.2	366.1	11.2	2.9	3.4	33.3	156.0	99.9+

*Slight effect on pollen. **Marked effect on pollen.

Summary

0............	25	86.4	128.9	1.6	24.4	4.4	18.7	1116	8.8	2.1	5.4	78.2	376.9	1.9
1............	76	89.1	101.8	1.1	18.8	4.4	14.7	827	9.0	2.2	4.8	63.4	266.2	5.6
2............	22	95.0	91.7	1.0	16.2	5.9	11.5	726	9.4	2.4	4.3	55.0	195.0	24.4
6 (Av.).......	33	97.1	94.5	1.0	17.7	3.8	10.3	560	11.7	2.7	4.3	55.0	209.2	82.4
13 (Av.).......	22	100.1	86.6	2.6	25.6	6.5	6.2	366	11.2	2.9	3.4	33.3	156.0	99.9+

It is at once apparent that these averages have acquired a real meaning. In most cases there is a definite and consistent trend away from Zea and upward or downward toward Tripsacum as the number of Tripsacum chromosomes increases. This occurs in nine of the twelve graphs. Two of the curves, those representing number of tillers and number of leaves, are of particular interest, for they show the conflicting effects of an unbalanced condition and an increase in the number of Tripsacum chromosomes. The former reduces vigor, and hence the number of tillers and leaves. The latter results in an increase in Tripsacum genes and hence should stimulate tillering and the production of leaves. In both of these characteristics there is first a decrease resulting from the addition of one extra Tripsacum chromosome, a further decrease resulting from the addition of another Tripsacum chromosome, little or no change produced by the addition of four more chromosomes, and finally an increase resulting from the addition of an average of seven more chromosomes. The result is a characteristic U-shaped curve. The curve for number of ears is also undoubtedly of this type, but some wide fluctuations are in evidence.

The genic effects of the Tripsacum chromosomes, uninfluenced by the unbalance, can in each case be measured by a comparison of the group averaging six Tripsacum chromosomes with the group averaging thirteen, for these two groups are theoretically in a similar state of unbalance, the first representing a departure from the balanced and vigorous Zea, the second a departure of the same degree from the balanced and vigorous triploid hybrid.

It is noted that in ten of the eleven characteristics which distinguish Zea and Tripsacum, the 13-chromosome group differs from the 6-chromosome group in the direction toward Tripsacum. In only one characteristic, leaf index, does this fail to hold true and this discrepancy is largely due to a single very unusual 4-chromosome plant with a leaf index of 42.0, which is completely outside the normal range of distribution.

Another characteristic common to all curves except the one for number of ears is the fact that two chromosomes show approximately twice the effect of one; but here the linear relationship ceases and the curve changes its slope, becoming, in every case except one, less steep. This is rather surprising, for in such characteristics as number of days to silking, height of stalk, number of tassel branches, and number of male spikelets, the increase in the degree of unbalance and the concentration of Tripsacum genes should theoretically act in the same direction and we should expect the slope of the curve to become steeper rather than otherwise. This, however, is certainly not the case; and with the exception of the three curves for number of tillers, number of leaves, and number of ears, which are U-shaped, all others follow the same general pattern as the curve on venation index, which is probably the best measure of the effects of an increase in the concentration of Tripsacum genes, since we should not expect it to be greatly influenced by chromosomal unbalance.

The nine curves, which appear to be of the same general type, have been averaged to produce the curve shown in Fig. 62. This was done by converting all actual values into percentages, considering the values for the group with no Tripsacum chromosomes as 0, and the group with 13 Tripsacum chromosomes as 72.2, with the intervening values computed accordingly. Any other arbitrary scale might have been chosen, and this particular one was used only because 72.2 represents the percentage that 13 is of 18, the maximum possible number of Tripsacum chromosomes.

The values so obtained are comparable and can be averaged. From these averages the curve in Fig. 62 has been drawn.

Here again, it is evident that two chromosomes have almost exactly twice the effect of one, the actual averages being 40.8 and 22.6, respectively. But six chromosomes do not have six times the effect of one, or three times

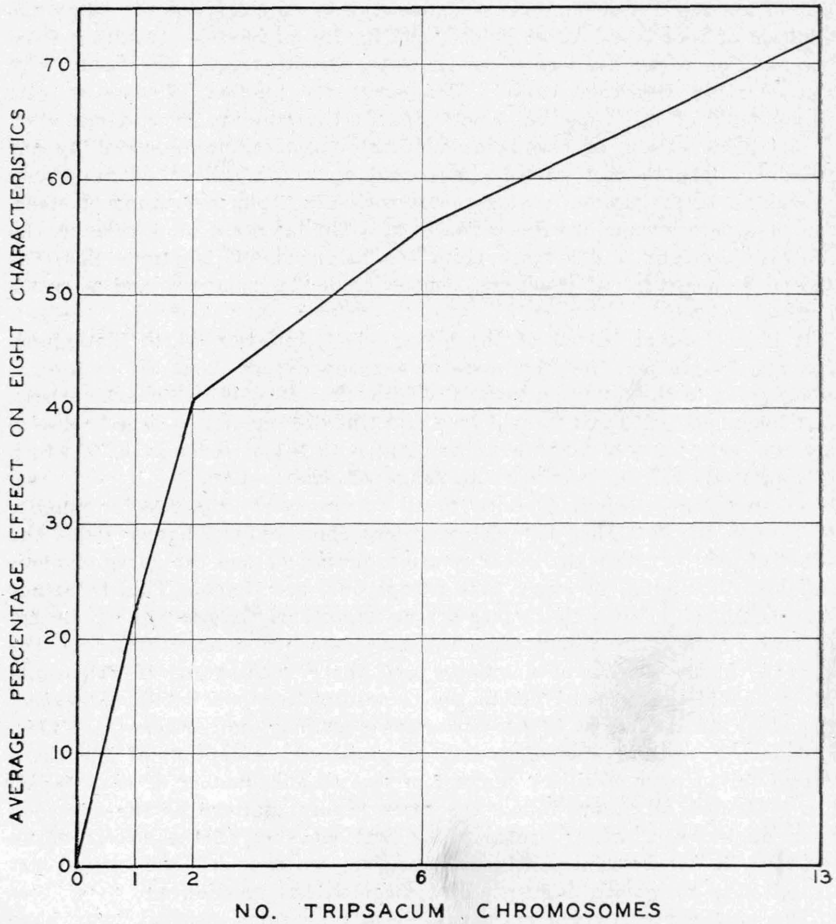

Fig. 62. The average effect of various numbers of Tripsacum chromosomes upon eight quantitative characteristics by which Zea and Tripsacum differ.

the effect of two. In fact the addition of four more chromosomes brings the average value up to only 55.8, an increase not quite as great as that resulting from the addition of a single chromosome in the first two instances. The addition of seven more chromosomes to bring the average up to thirteen has approximately the same effect as adding four to the first two.

It seems apparent from the curves in Fig. 61, and the average curve in Fig. 62, that an increase in number of Tripsacum chromosomes above a number of two is accompanied by diminishing returns, so far as changing the various characteristics in the direction of Tripsacum is concerned. This can be interpreted in at least two ways. We have already discussed the possibility that the two groups having one and two extra chromosomes are the product of a random assortment of two particular Tripsacum chromosomes which pair regularly with the Zea chromosomes and accompany them during meiosis to one pole or the other. It may be that these two chromosomes have a greater effect than any others in the Tripsacum complex, and there is some evidence of this in the fact that one of these is the longest of the Tripsacum chromosomes. Another interpretation that occurs to us is that we are dealing with partially dominant genes having similar effects. The first dominant genes introduced would thus have the maximum effect and additional genes relatively less. If dominance were complete, the first gene would produce the maximum possible effect, and additional genes would have no effect whatever. If no dominance were displayed, the relationship would be expressed by a straight line. Partial dominance should result in a condition which is intermediate between these two extremes.

If it is dominance that is being measured by these data, the results are certainly not in agreement with Fisher's hypothesis that dominance has come about through the action of modifiers. If the number of modifiers is large, and the modifying genes are scattered more or less at random over all the chromosomes, then the larger the number of Tripsacum chromosomes which a plant possesses, the larger the number of modifiers for dominance which would be present. For example, we may assume that a certain gene A, borne on chromosome No. 1 in Tripsacum, is dominant in Tripsacum because of modifying genes scattered at random over all 18 of the Tripsacum chromosomes. When this single chromosome with its gene A is superimposed upon the genetic complex of Zea, the gene A is only partially dominant because it is accompanied only by such modifying genes as may reside in chromosome No. 1. But as additional Tripsacum chromosomes are added to the complex, more and more modifiers of A are brought in; the gene A should become more and more dominant in its effect, and the curve should rise proportionately with each additional increment of Tripsacum chromatin. What has actually occurred is directly contrary to what we should expect from this hypothesis, for each successive addition of Tripsacum chromatin has a smaller effect than the preceding one.

It is impossible, with the data at hand, to determine which of these two alternative interpretations which we have considered is most acceptable. There is some evidence in favor of the first in the fact that one of the extra Tripsacum chromosomes involved in groups two and three is the longest of the entire Tripsacum complex and hence might well be expected to carry more Tripsacum genes. On the other hand, the fact that the change from six to thirteen chromosomes produces no more effect than a change from two to six, would indicate that an accumulation of genes exhibiting partial dominance is involved.

In any case, however, it is quite clear that an increase in the estimated average number of Tripsacum chromosomes is accompanied by a change in all characteristics of the plant, away from Zea and in the direction of Tripsacum. This does not mean, however, that all eighteen Tripsacum chromosomes bear genes which affect all characteristics in the direction of Tripsacum. The results are equally well explained by assuming that the genes which distinguish the two genera are concentrated on a few chromosomes, and the increase in effect which accompanies the increase in number of Tripsacum chromosomes is purely the result of the increased frequency with which these particular chromosomes are included in the sample. Thus if all the genes were concentrated on one chromosome and the assortment of chromosomes were a random one, this particular chromosome would be included in 1/18 of the plants with one extra chromosome, 2/18 of the plants with two extras, etc. There is no reason for believing that this is actually the case. On the other hand, there is no reason for assuming that all chromosomes are equal in their effects upon all characteristics. It would seem more likely that one chromosome might carry more genes affecting time of maturity than any other, another more genes affecting number of tassel branches. In fact, it is quite likely that the genetic complex of Tripsacum genes would include genes which operate in different directions, some in a direction toward Zea, others in a direction away from Zea. We have some evidence from several characteristics that this is actually the case.

In this population of 178 plants there were five which lacked the central spike of the tassel. The terminal inflorescence of Tripsacum always lacks this structure, the maize tassel always exhibits it. Of the five plants in the segregating population in which it was absent, one possessed one extra Tripsacum chromosome, one possessed two and the remaining three possessed ten or more. Yet when all eighteen Tripsacum chromosomes are present, as in the parental triploid hybrid, the central spike is also present. Here is a case where a few Tripsacum chromosomes have a greater effect in the direction of Tripsacum than all of them combined. This indicates that Tripsacum, which does not have a central spike, nevertheless carries some genes for this structure just as does corn which exhibits a central spike. But it also has genes which tend to suppress the central spike and in pure Tripsacum these genes, or their effects, are the predominating ones. In a plant with 20 Zea chromosomes and 18 Tripsacum chromosomes, the genes for the development of the central spike predominate and the structure is always present. But in the succeeding generation, plants with as few as one or two Tripsacum chromosomes may lack the central spike. This suggests that one or two particular chromosomes carry a concentration of genes for suppression of the central spike and that these one or two chromosomes, when not neutralized by genes working in an opposite direction on other chromosomes, are effective enough to be dominant over the genes of maize which condition the development of the central spike.

A similar situation exists in the case of horny and membranaceous glumes. When all 18 Tripsacum chromosomes are present the glumes are horny. Yet the presence of only one extra chromosome can produce horniness in the glumes, while plants with as many as 10 extra chromosomes may still have membranaceous glumes. These facts are interpreted as an indication that several of the Tripsacum chromosomes, apparently less than half of them, carry genes for horniness of the glumes while the remaining chromosomes lack these genes.

Another characteristic which behaves in the same fashion is the presence of pistillate spikelets in the tassel. Tripsacum always has pistillate spikelets in the terminal inflorescence; maize normally does not, although certain genetic types of maïze may exhibit this condition regularly, and almost all varieties will show it under certain unfavorable environmental conditions. In the segregating population of 178 plants, 10 were found with pistillate spikelets in the tassel. With regard to the number of Tripsacum chromosomes possessed, the 10 plants were distributed as follows: two had one Tripsacum chromosome, one each had two, four, five, and six, two had nine, and two had ten or more. In other words, the group of plants with an average of six Tripsacum chromosomes had more plants with pistillate spikelets in the tassel than the group with an average of thirteen Tripsacum chromosomes. The parental triploid hybrid with all eighteen Tripsacum chromosomes was completely lacking in pistillate spikelets in the tassel.

Finally, we call attention to a comparison of the most Tripsacum-like plant (10-10) in Fig. 59 with the parental hybrid Fig. 43. Here is a plant in the segregating generation, presumably with less than 18 Tripsacum chromosomes which is much more like Tripsacum in some of its vegetative characteristics than the plant possessing all 18 of the Tripsacum chromosomes.

All of these facts and observations, it appears to us, are subject to the same interpretation—that certain Tripsacum chromosomes have a greater effect in the direction of Tripsacum than do all of them combined. This is probably the situation which we should have expected had we given the matter any previous consideration, for if we are willing to go back far enough we must assume a common ancestor for both Zea and Tripsacum. When the two genera first diverged from a common ancestor, they must have had many genes which were identical. The fact that they can still be hybridized indicates that they still have genes in common. And though Tripsacum has accumulated genes which caused it to develop into a plant quite different from the maize plant, it also possesses genes which would, if not neutralized by other genes, cause it to be more like maize than it actually is. The Tripsacum plant that we see today is the net product of genes with opposing forces, and if we could separate the two types of genes by selection we would undoubtedly be able to develop plants of Tripsacum which deviate less widely or more widely from Zea than does the present form. If the number of genes involved in the expression of any one characteristic is relatively small, we cannot expect each chromosome to carry a random sample of the genes involved. By chance assortment alone, some chromosomes would carry more genes affecting a certain characteristic than would others. There is no necessity for assuming that there has been a "division of labor" among the chromosomes, or that we have a tendency toward "genus chromosomes" which differentiate the genera, as the sex chromosome differentiates the sexes in many organisms. But it is clear, we think, that so far as individual characteristics which differentiate these genera are concerned, the genes which govern the expression of several of these characteristics are concentrated or confined to a relatively small number of chromosomes. This fact and the fact that a small number of Tripsacum chromosomes have a greater effect, relatively than a large number, are both important in connection with the possibility to be discussed later, that teosinte has originated as the result of superimposing a small amount of Tripsacum chromatin upon the chromosome complex of Zea.

Segregates with a 2n + 1 Complex.

The extra Tripsacum chromosomes were lost very rapidly from this population in later generations. None were transmitted through the pollen; in fact plants with more than two Tripsacum chromosomes seldom dehisced their pollen, while plants with still larger numbers frequently failed to exsert their anthers. Though the extra Tripsacum chromosomes were transmitted through the ovules to some extent, there was, even here, a marked selective action against them, not only in the development of the seeds but also in germination and survival. In this respect they were quite similar to trisomic maize (cf. Rhoades and McClintock 1935). We had planned, by repeated backcrossing to a uniform inbred strain of corn, to develop eighteen distinct 2n + 1 stocks alike in their Zea germplasm but differing in their extra Tripsacum chromosomes, and thus to make on accurate comparison of the effects of the various Tripsacum chromosomes, and also to determine by crosses with appropriate recessive stocks of maize, the location on the chromosomes of the dominant alleles in Tripsacum. This appeared to provide a means of making a chromosome map of Tripsacum, even without having available any workable recessive genes in this genus. Unfortunately, however, the selective action against the unbalanced 2n + 1 plants was so great that the various stocks were, one by one, lost from our cultures, and only one has been maintained until the present time. This one, however, is of particular interest because the extra Tripsacum chromosome is marked by the dominant allele of the *su* gene for sugary endosperm.

The original hybrid of Zea x Tripsacum was homozygous non-sugary, since Tripsacum is always starchy and the maize parent of the cross was also starchy. A number of the seeds produced by this hybrid, however, were the result of pollinating with a stock homozygous for sugary endosperm; so that in the next generation, represented by the triploid hybrid (Zea x Tripsacum) x Zea, the plants were heterozygous for sugary endosperm and of the composition $Su^Z\ Su^T\ su^Z$, the superscript indicating whether the gene had been received originally from Tripsacum or from Zea. These hybrids were now pollinated by sugary maize $su^Z\ su^Z$, a procedure which might be expected to result in four kinds of seeds, as follows: $Su^Z\ su^Z$, $Su^Z\ Su^T\ su^Z$, $Su^T\ su^Z\ su^Z$, $su^Z\ su^Z$.

Because many of the seeds were small and slightly aborted, and perhaps also because the Su^T allelomorph was not so completely dominant as Su^Z, there was some difficulty in classification. Six ears were obtained, however, in which the segregation of starchy and sugary seeds was reasonably clear-cut, and in which the two types were separated with the results shown in Table 17.

Table 17. Segregation for sugary endosperm in the triploid hybrid $Su^Z\ Su^T\ su^Z$ pollinated by $su^Z\ su^Z$

Ear No.	Total seeds	Sugary	
		No.	Per cent
494-1	23	9	39.1
494-1-3	23	9	39.1
494-2-1	25	6	24.0
494-2-2	22	6	27.3
494-2-3	15	5	33.3
497-1-1	14	6	42.9
Total and average	122	41	33.6

Since the cytological studies had indicated a regular pairing and separation of the Zea chromosomes, we may assume that half of the total number of seeds, approximately 61 of them, were starchy because they had received the allelomorph Su^Z. Of the remaining 61, 41 were pure sugary because they had received no *Su* gene from either Tripsacum or Zea and the remaining 20 were starchy because they had received the Su^T allelomorph from Tripsacum. It is evident, then, that 32.8 per cent of the functional gametes, or approximately one-third, carry the Su^T gametes from Tripsacum. This fact, however, is susceptible to two interpretations; it may mean that a particular Tripsacum chromosome having the Su^T gene is present in one-third of the functional gametes, or it may indicate that there are several Tripsacum chromosomes having an Su^T gene and that one or more of these are present in one-third of the functional gametes.

The data already presented (p. 137) on the distribution of plants with various numbers of extra Tripsacum chromosomes indicate that the first interpretation is probably the correct one. We have shown that there is a great excess of plants with 0, 1, or 2 Tripsacum chromosomes above the numbers that might have been expected, or could have occurred, from random distribution of the eighteen chromosomes. We have also presented some evidence which indicates that the group of 76 2n + 1 plants comprised two rather distinct classes — one which exhibited a marked Tripsacum effect on the glumes accompanied by a marked reduction in size of half of the pollen grains; the other which exhibited only a slight effect in the pollen and glume characteristics. The latter group is apparently associated with the chromosome which bears the Su^T gene, for in this group the segregation for sugary seeds was seldom clear-cut, and the ratios are usually either "high" sugary or "low" sugary. Furthermore, in this group of 34 plants, 25 of which set seed, there was not a single unquestionable homozygous sugary plant. There was one plant in the 25, classified as pure sugary with a question mark following the notation, which indicates that all of the seeds were not good sugary. In the other group of 2n + 1 plants comprising a total of 42 plants, there were 27 which had set seed. Of this number, 6 were definitely homozygous sugary. Furthermore, the segregation for sugary endosperm in the remainder was usually clear-cut and the ratios good.

If the Su^T gene is associated with the chromosome having only a slight effect upon pollen and glumes, then all the 2n + 2 plants should carry this chromosome and all should be segregating for sugary, with disturbed ratios. This appears to be the case, for though two of the plants are classified as pure sugary, the number of seeds, 11 in each, is too small to establish this clasification and in the remaining plants the classification is difficult and the ratios appear to be disturbed. It is very difficult to determine this accurately because the Su^T allele is evidently not completely dominant and when a plant is segregating for both Su^T and Su^Z there is a deficiency of good sugary seeds; but it is almost impossible to make an accurate separation of the various combinations which occur, and we can only say that the ratios appear to be disturbed.

The results, however, are all explicable by assuming that there is only one Tripsacum chromosome which bears an allele of the *su* gene of maize and that this particular chromosome is one of the two which regularly pairs with the maize chromosomes and is thus transmitted to a large proportion of the progeny. Our data on segregation for sugary endosperm in the parental triploid hybrid show that the Su^T allele is present in approximately one-third of the seeds produced; the data on the succeeding generations show that the chromosome which has a slight effect on pollen and glumes, and usually a disturbing effect on starchy-sugary segregation, and hence is presumably the one bearing the Su^T gene, occurs in 56 of the 123 plants having 0, 1, or 2 Tripsacum chromosomes, a ratio slightly higher than 1 in 3, but approaching it.

Finally, we have isolated from the group of 34 2n + 1 plants several plants which are "high" sugary or "low" sugary. The former is expected when the plant is heterozygous only for the Su^T gene, which is transmitted to half of the ovules but which (because of the selective action against the 2 + 1 gametes) appears in less than half of the seeds. The "low" sugary ratios should occur when both Su^T and Su^Z are segregating. Half of the seeds should be starchy because they have received Su^Z, and about a third of the remainder should be starchy because they have received Su^T. Plant No. 10-33 was definitely high sugary, for it bore 32 starchy and 127 sugary seeds. Plant No. 10-19 was suspected of being low sugary, for it bore 33 starchy and 18 sugary seeds.

Planting the starchy seeds from a high sugary ear should result in only high sugary ratios in the next generation. Unfortunately, only one plant was brought to maturity, but this single plant when pollinated with pure sugary produced 5 starchy and 118 sugary seeds. The starchy seeds from low sugary plants should give rise to three types: normal sugary resulting from the segregation of Su^Z and *su*, high sugary resulting from the segregation of Su^T and *su*, and low sugary resulting from the segregation of Su^T, Su^Z and *su*. Only two plants from this progeny were matured, but both of these, unlike their low sugary parent, were high sugary. One produced starchy and sugary seeds in the ratio of 86:125, the other in the ratio 14:18. The latter is not significant deviation from a 1:1 ratio, but the ear was classified as high sugary because the gene Su^T was obviously the one involved, a conclusion dictated by the fact that some sterility was evident and by the fact that the starchy seeds were smaller than the sugary seeds though the reverse is usually true.

We have continued both of these stocks for several years, always by crossing heterozygous Su^T su^Z, 2n + 1 plants by pure sugary; and though we have obtained many ears in which classification of the starchy and sugary seeds was virtually impossible, we have obtained others in which the segregation was fairly clear-cut. The segregation for starchy and sugary seeds in the latter is tabulated in Table 18. It will be noted that in every case except one, Plant No. 10-19-1-1, there is an excess of sugary seeds; and the average percentage of sugary seeds is 65.3. The starchy seeds are usually smaller than the sugary seeds on the same ear. This is shown by the weights in Table 19 for the seeds from five of these ears and is illustrated in Fig. 63. Sugary seeds usually weigh much less than starchy seeds on the same ear. Mangelsdorf (1926) found them to weigh only 88.5 per cent as much; Kiesselbach (1926) in similar studies found the weight of sugary seeds to be 85.8 per cent as much as those of starchy seeds in the same stocks. But in this stock where the starchy seeds are the product of the Su^T gene from Tripsacum, the situation is completely reversed, and the starchy seeds weigh only 86.6 per cent as much as the sugary seeds on the same ear.

This stunting of the seeds is probably not so much the effect of the Su^T allele as it is of the unbalanced condition resulting from the extra

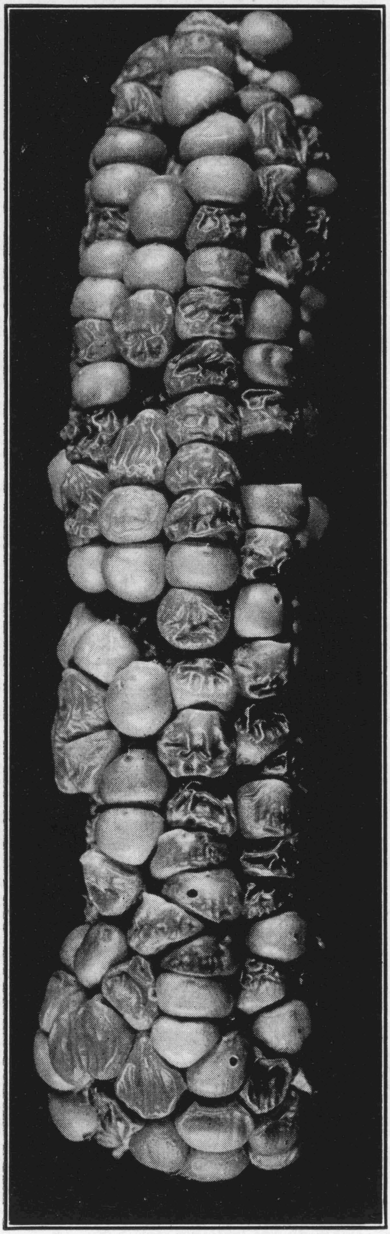

Fig. 63. Ear from a 2n+1 plant in which the extra Tripsacum chromosome bears an allele of the *su* gene from maize. Starchiness of seeds indicates presence of extra Tripsacum chromosome. Note irregular appearance of ear due to failure of part of the ovules to develop, and reduced size of starchy 3n+2 endosperms.

chromosome on which Su^T is borne—a circumstance which also accounts for the deficiency of starchy seeds. It is assumed that half of the ovules receive the extra Tripsacum chromosome, but that some of these fail to survive. This assumption is borne out by the fact that ears from plants with the extra Tripsacum chromosome are always irregular in appearance because of the gaps left by the failure of seeds to develop. The percentage of surviving seeds which have received the Su^T gene, (34.7) agrees so closely with the 32.8 per cent assumed to have received an allele from Tripsacum in the triploid hybrid (see Table 18) that it suggests once more that there is only one allele for *su* in the entire Tripsacum complex and that this particular Tripsacum chromosome is the one which bears it.

Table 18. Segregation for sugary endosperm in 2n + 1 plants in which the extra Tripsacum chromosome carries an allele of the sugary gene

Ear No.	Total seeds	Sugary	
		No.	Per cent
10–19–1	211	125	59.2
10–19–2	32	18	56.2
10–33–1	177	118	66.7
10–19–1–1	137	62	45.3
10–19–1–2	144	85	59.0
10–19–1–3	330	194	58.8
10–19–1–4	23	17	73.9
10–33–1–1	255	179	70.2
10–33–1–2	193	142	73.6
10–33–1–3	212	141	66.5
10–33–1–4	196	137	69.9
10–19–1–2–1	187	155	82.9
10–19–1–3–1	167	114	68.3
10–33–1–1–1	95	50	52.6
10–33–1–2–1	174	121	69.5
10–33–1–2–2	145	78	53.8
10–33–1–2–3	66	56	84.8
Total and average	2744	1792	65.3

Table 19. Weights of starchy and sugary seeds on ears from 2n + 1 plants

Ear No.	Average weight, mg.		Wt. *Su*/wt. *su*
	Su	*su*	
10–19–1	61	66	92.4
10–19–2	101	110	91.8
10–19–1–2–1	159	179	88.8
10–19–1–3–1	213	257	82.9
10–33–1–2–2	149	176	84.7
Average	136.6	157.6	86.7

We have throughout this discussion assumed that the starchy gene in Tripsacum, Su^T, is a different allele of sugary from the starchy gene in Zea, Su^Z. The only evidence which we have had for this assumption is the fact that Su^Z is always completely dominant and Su^T is seldom so.

The dominance of *Su*^{Z} is so pronounced that no chemical differences can be detected in seeds of the composition *su su Su* which result from the pollination of sugary by starchy and those of the composition *Su Su Su* which are pure starchy (Lindstrom and Gerhardt 1926). In other words, in the triploid endosperm tissue of maize, one dose of *Su* is as effective as three doses. In the case of *Su*^{T}, however, all of the starchy seeds which we have studied have been of the composition *Su*^{T} *Su*^{T} *su*. Yet in spite of the double dose of the *Su*^{T} gene dominance is not complete. There are always some seeds which are intermediate between starchy and true sugary, and even the seeds classified as true starchy usually exhibit a trace of wrinkling.

If the starchy gene in this stock is borne on the extra Tripsacum chromosome, then the starchy seeds when planted should give rise only to 2n+1 plants and the sugary seeds only to normal 2n plants. This has usually been the case, but there have always been some exceptions—a few of the sugary seeds producing plants with extra chromosomes and variable pollen; a few of the starchy seeds producing plants with normal pollen and no extra chromosomes. These results would indicate that an exchange of chromatin has sometimes occurred between the extra Tripsacum chromosome and one of the Zea chromosomes, so that the *Su*^{T} gene is transferred to a Zea chromosome or the *su* gene to the Tripsacum chromosome. We could never be certain, however, that this had occurred because our classification of starchy and sugary seeds was never completely satisfactory. But in 1936 we obtained one ear (from plant No. 10-33-1-1-1 in Table 18) in which there was absolutely no question about the classification, at least of the pure sugary seeds. The seeds classified as starchy, of which there were 45, were divided into three groups—one called "good starchy," consisting of 17 seeds which would under any circumstances be considered starchy; one called "starchy-sugary," consisting of 11 seeds which were starchy in appearance but showed some slight wrinkling; and a third called "sugary-starchy," consisting of 17 seeds which were definitely wrinkled but showed a considerable amount of opaque tissue, similar to the so-called pseudo-starchy seeds found in many sweet corn varieties.

Chromosome counts of plants grown from these seeds were made both in root tip smears and pollen mother cells. Except one in the sugary-starchy class which had only 20 chromosomes, all plants from any type of starchy seeds showed an extra chomosome. These associated regularly to form ten approximately normal pairs except for a slight terminal dissociation in the long arm of chromosome 2 (Figs. 64A, G, 65A). This we interpret to mean that a short piece of the Tripsacum choromosome, a piece which carried the *Su*^{T} gene, had been exchanged for a short section of the end of chromosome 2.

All of the plants originating from sugary seeds, however, were 20-chromosome plants with no Tripsacum chromosomes. Some irregularities in pairing relationship were exhibited, however, as is shown by the quadrivalent in Fig. 67E; and at least one of these 2n plants showed definite

Tripsacum influence in its leaves, which were stiffer and more glossy than those of pure maize.

Also, there were some cytological irregularities in the 2n+1 plants in addition to the presence of an extra chromosome. These are illustrated in Figures 64B, 65B and 67A, the first two of which show association between chromosomes 1 and 4, and the second a chromosome chain at diakinesis.

The behavior of the extra Tripsacum chromosome in this generation is extremely interesting. We had in previous generations observed association of the Tripsacum chromosome with Nos. 1 and 4 of Zea. In this generation association with Nos. 5 and 9 were observed in addition.

From cytological studies of many investigators, an abundance of evidence has accumulated showing that chromosome pairing at diakinesis usually is associated with homology and chiasma formation. Non-homologous pairing at earlier stages may occur frequently in maize, but when it does, the members usually dissociate before diakinesis, because of a lack of chiasmata. If two chromosomes are weakly associated at diakinesis and rarely dissociated, a slight homology may be assumed. It is possible that non-homologous chromosomes may be paired at diakinesis as a result of crossing-over and chiasma-formation.

The cytological phenomena observed in this 2n + 1 stock in 1937 must be interpreted in light of the fact that the extra chromosome which we have been calling a Tripsacum chromosome has occupied the same nuclei with Zea chromosomes for six plant generations, during which it may have exchanged segments of chromatin with one or more Zea chromosomes. Such an exchange would in itself probably be a strong indication of homology, but there is the possibility that segmental interchanges or translocations* have occurred. With these considerations in mind we may examine the results.

The Tripsacum chromosome retained by this 2n+1 strain was found paired with chromosome 1 more frequently than with any other. The pairing was a little more frequent with the short arm (Fig. 66A) than the long (Fig. 66C), but pairing with both arms of one unidentified chromosome did occur (Fig. 65G). Whether this pairing is homologous or non-homologous is problematical, but the frequency with which it occurred indicates that in some former generations after F_1, exchange of segments between the Zea and Tripsacum chromosomes occurred, or that there originally were segments in certain Zea chromosomes that were homologous with the Tripsacum chromosome, because diakinesis usually

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*At the present time we have no way of determining whether these exchanges of segments occurred by translocations or by crossing-over. When trivalents were found the two members that synapsed most completely usually were of similar lengths, although the differences were often great enough to be obvious. This similarity in length would seem to indicate that the phenomenon was of the nature of crossing-over accompanied by a considerable degree of homology. On the other hand it is possible that figures chosen for detailed study were unwittingly selected in favor of those in which the most closely synapsed members were of similar lengths. It certainly is true that the members' being of similar lengths simplified the identification of the maize chromosomes. This phenomenon deserves further study. McClintock (1933) studied a similar phenomenon in maize and stated that it may be an abnormal expression of the cross-over process. However, since our results do not clearly indicate the process involved, our reference to it as "segmental interchange" or "translocation," is not intended to imply its exact nature.

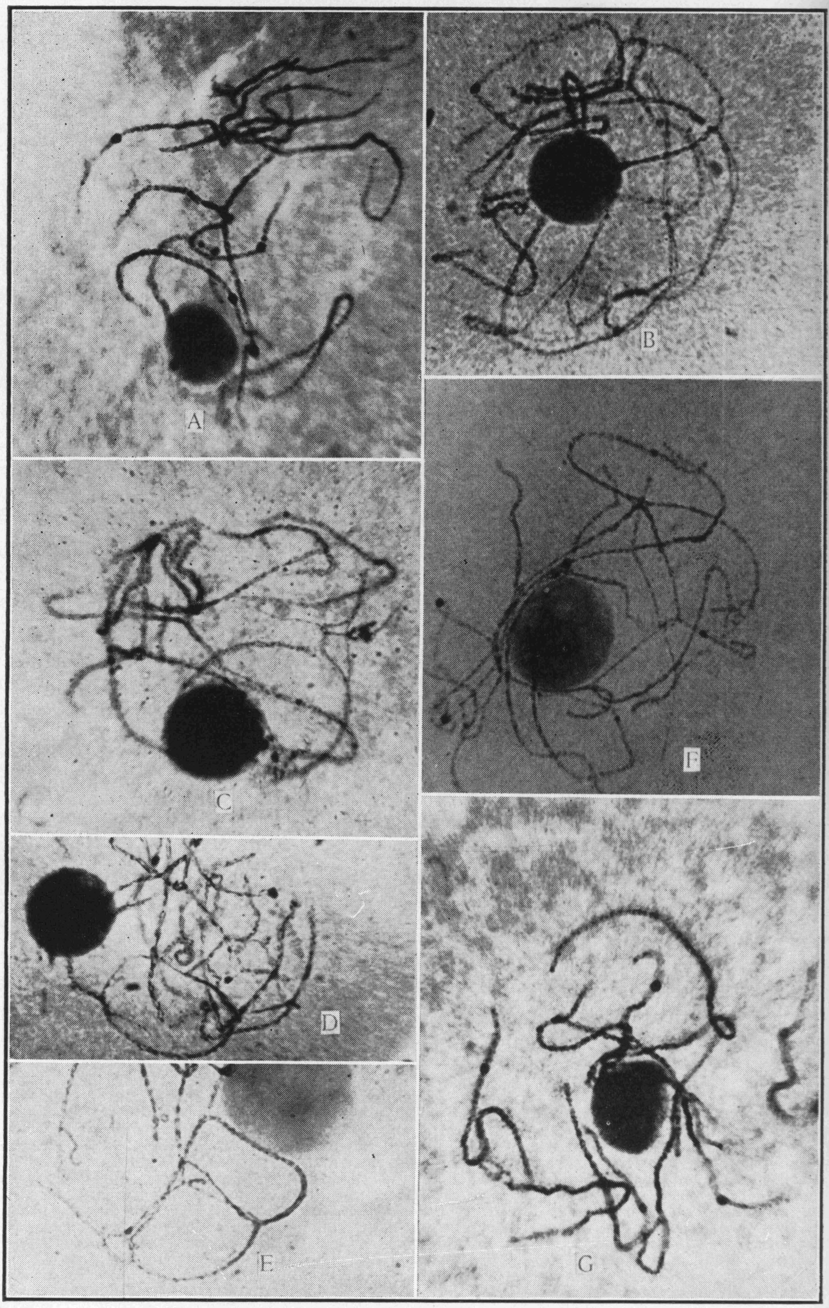

Fig. 64. Chromosomes of 2n+1 hybrids and their segregates; X 1000. A. 10 chromosomes normally synapsed except in a short terminal region of chromosome 2. B. Tripsacum chromosome incompletely synapsed with Zea chromosomes 1 and 4. C. Tripsacum chromosome synapsed with the short arm of Zea chromosome 4. D. Tripsacum chromosome incompletely synapsed with short arm of Zea chromosome 4. E. Tripsacum chromosome incompletely synapsed with long arm of Zea chromosome 4. F. Tripsacum chromosome incompletely synapsed with long arm of Zea chromosome 9. G. Failure of synapsis in terminal segment of chromosome 2; similar to A and taken from the same plant.

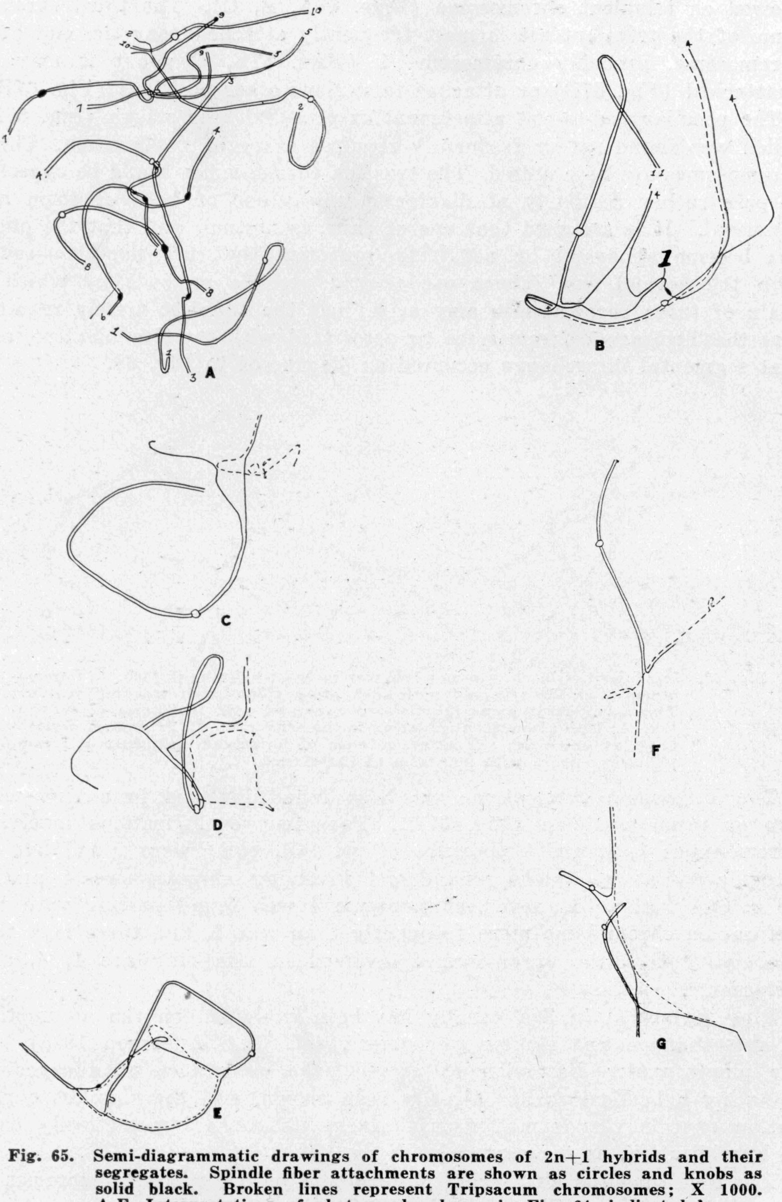

Fig. 65. Semi-diagrammatic drawings of chromosomes of 2n+1 hybrids and their segregates. Spindle fiber attachments are shown as circles and knobs as solid black. Broken lines represent Tripsacum chromosomes; X 1000. A-F. Interpretations of photographs shown in Fig. 64. indicated by corresponding letters. G. Tripsacum chromosome incompletely synapsed with both arms of one Zea homolog and with the long arm of the other. (The Zea chromosome possibly is No. 4.)

showed on trivalent chromosome (Figs. 67A, B, C). The third chromosome of the trivalent set is most frequently attached near the end of a chromosome, probably chromosome 1 (Figs. 67B, C); but it may be unattached (Fig. 67D) or attached in various other positions (Fig. 67H).

The peculiar end-to-end attachment at post-diplotene stages (Fig. 67A) which was found rather frequently requires a special explanation. Three chromosomes are here united. The two Zea chromosomes would be expected to pair rather regularly at diakinesis unless one or both of them are abnormal. It is assumed that one of them is normal, and that the other has become abnormal by acquiring segments that are non-homologous with the normal one. There are several possible methods by which a chain of three chromosomes may arise; but the simplest merely requires that the Tripsacum chromosome be associated with the Zea bivalent, and that segmental interchange occurred as diagramed in Fig. 68.

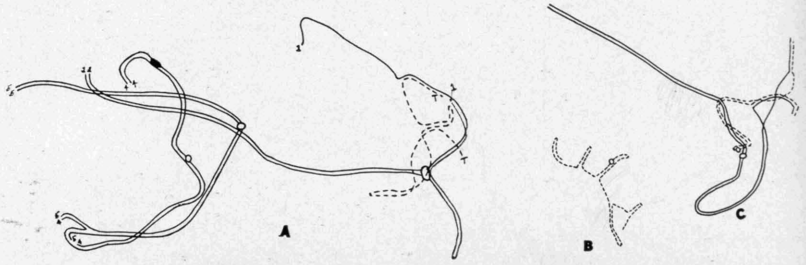

Fig. 66. **Irregularities in chromosome behavior in 2n+1 hybrids; X 1000. A. Chromosomes 4 and 5 synapsed with each other along short terminal regions; Tripsacum chromosome incompletely synapsed with short arm of chromosome 1; both phenomena occurring in the same cell. B. Tripsacum chromosome as univalent. C. Opposite ends of Tripsacum chromosome incompletely synapsed with long arm of chromosome 1.**

The Tripsacum chromosome was also found involved in a ring with two or three bivalents (Fig. 67F). Pachytene configurations involving chromosomes 1, 4, and Tripsacum (Figs. 64B, 65B) were found but an irregularity at pachytene was found involving chromosomes 4 and 5 (Fig. 66A), also. However, chromosome 4 was found pairing with the Tripsacum chromosome more frequently than was 5, and there is a fair probability that the chromosomes involved in this ring are 1, 4, and Tripsacum.

Ring formation in Zea usually has been explained on the assumption of interchanges and similar phenomena (cf. E. G. Anderson 1935). In the plants under discussion at present, the occurrence of allosyndesis following hybridization has already been shown, and the simplest explanation of this ring-formation is to trace its cause hypothetically back to hybridization, as diagramed in Figure 69.

The fact that the Tripsacum chromosome paired with chromosomes 1, 4, and even others (Figs. 64B-F, 65B-G), is not particularly surprising, because it may have borne genes identical or allelemorphic to the genes on several Zea chromosomes; or after repeated backcrossing to Zea

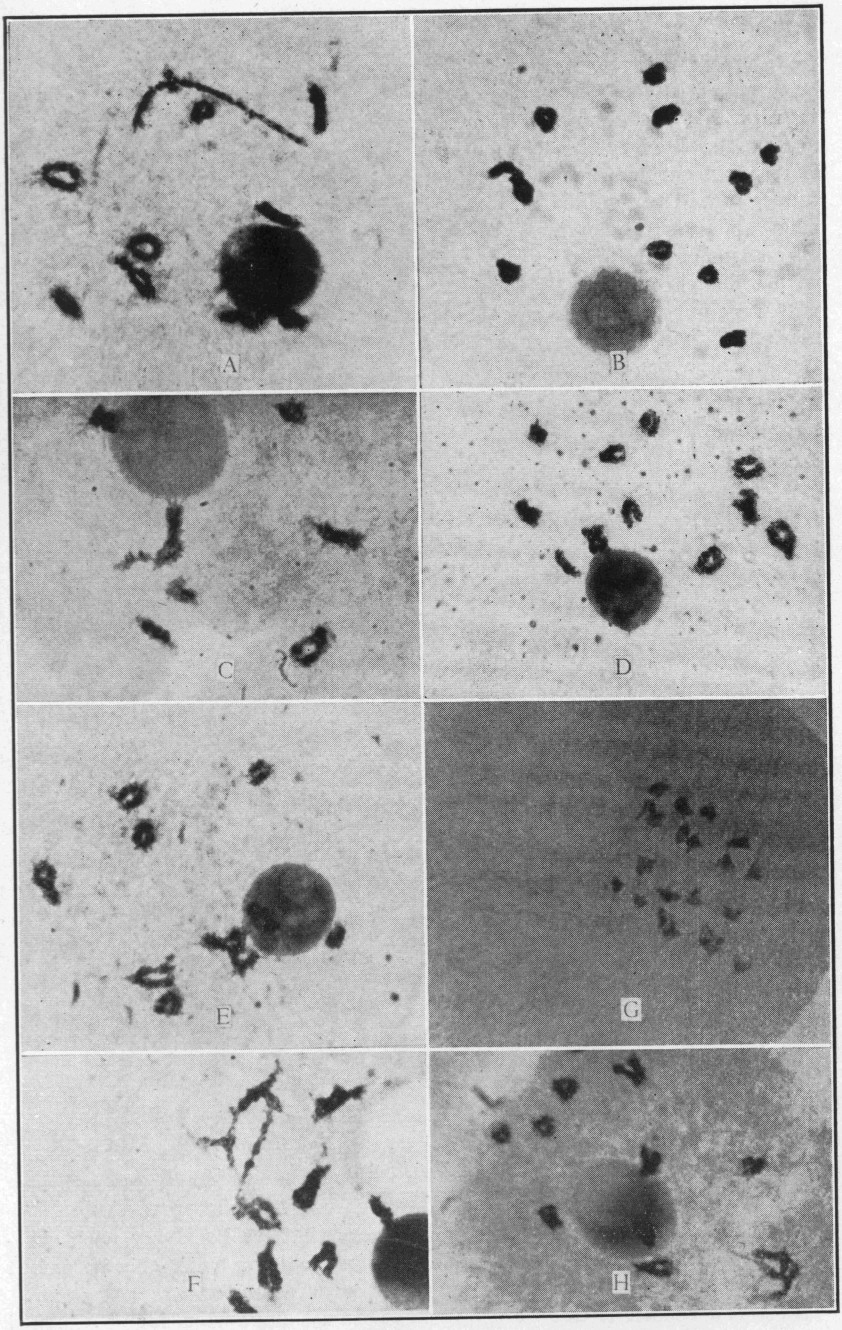

Fig. 67. Post diplotene stages of division-I in $2n+1$ hybrids and their segregates; X 1000. A. 9 bivalents and a trivalent with its members attached end to end forming a chain. B. Trivalent with one Tripsacum member attached to the end of the two synapsed homologs. C. same; third, terminally attached member much smaller than the synapsed homologs. D. 10 bivalents and a Tripsacum univalent. E. 8 bivalents and a quadrivalent. F. A ring of 5 chromosomes and 8 bivalents, possibly attached to a third bivalent below; one of the bivalents not included in the photograph. G. Anaphase showing 10 chromosomes going to the upper pole and 11 to the lower, the latter group including 2 bivalents. H. 9 bivalents and a trivalent.

it may have exchanged segments with the various chromosomes and arms. Since every Zea chromosome in these plants has its homolog, the Tripsacum chromosome would not compete strongly in the pairing activity unless it had exchanged segments with one particular Zea chromosome to such an extent that most of its content was identical with that Zea chromosome. But, instead, it probably paired and exchanged segments with other chromosomes as well as with number 1, making regular pairing with any part of chromosome 1 or with any particular chromosome quite unlikely. The frequent dissociation of the Tripsacum chromosome from the Zea bivalent (Figs. 66B, 67D) and its association with bivalents other than number 1 (Figs. 64B-E, 65B-E) shows that its homology with chromosome 1 is not especially great, even after pairing with chromosome 1 to a greater or less degree for six plant generations.

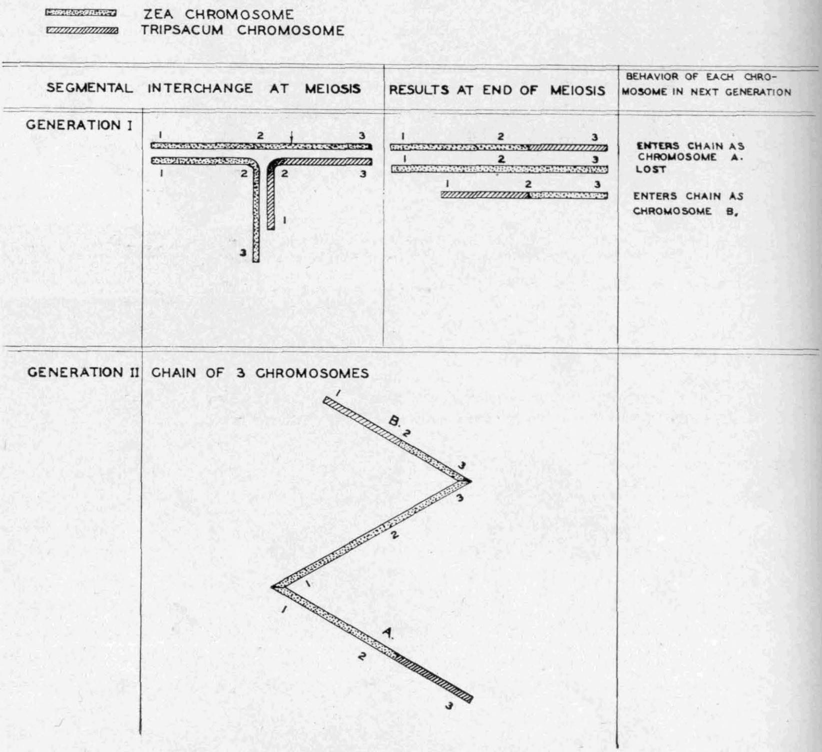

Fig. 68. **Scheme showing a possible method by which a chain of 3 chromosomes may occur after one exchange of non-homologous segments.**

On a few occasions two pairs of chromosomes have been found attached at pachytene (Fig. 66A) and diakinesis (Fig. 67E) without an extra chromosome or piece being distinguishably associated with them. The two pairs shown in Figures 66A are Nos. 4 and 5, and it is assumed that

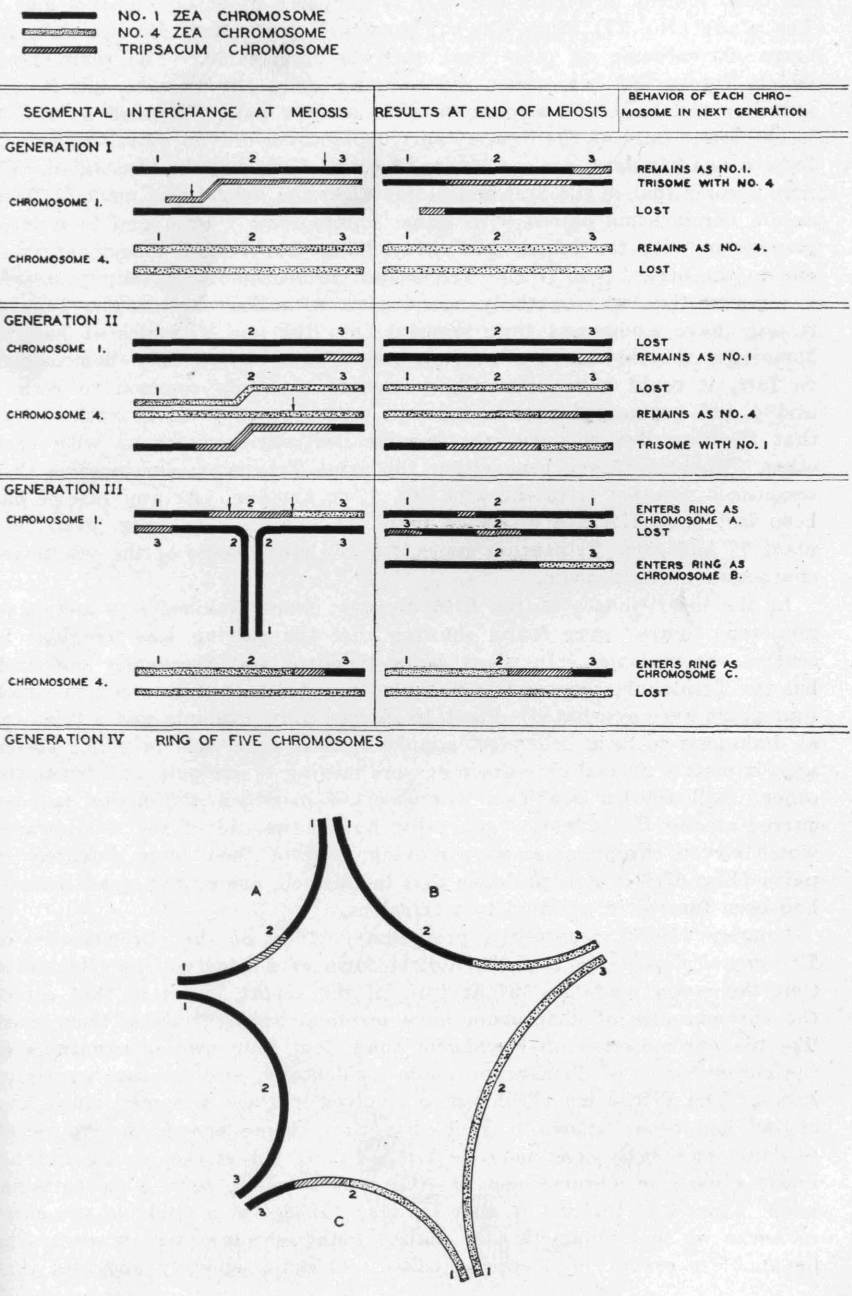

Fig. 69. Scheme showing a possible method by which a ring of 5 chromosomes may occur as a result of backcrossing accompanied by exchange of non-homologous segments.

the quadrivalent in Figure 67E also is composed of chromosomes 4 and 5. The plant (No. 77) from which Figure 67E was taken did not have an extra chromosome or piece that was distinguishable. The plant from which Figure 66A was taken did have an extra chromosome, but it was found in the same cell associated with another pair, identified as No. 1, in the lower part of the figure. Our explanation of two pairs' uniting to form a quadrivalent, as in Figures 66A and 67E, may be illustrated. We may assume that in the first generation after the hybrid was made, a Tripsacum chromosome paired with either chromosome 1 or 4 and in a later generation with the other; and in so doing transferred a segment from one to the other. Or, if the Tripsacum chromosome originally possessed a segment that was partially homologous with Zea chromosome 1 or 4, it may have exchanged that segment into the one to which it had no homology, thereby making chromosomes 1 and 4 partially homologous. In fact, it could have originally possessed segments common to both 1 and 4 and exchanged such a segment with one of them in such a way that the two Zea chromosomes became partially homologous with each other. This may have been either the same Tripsacum chromosome that sometimes forms a trivalent with No. 1, or another. At any rate it has been lost from the line of which plant 77 is a member (Fig. 67E), but plant 77 had some Tripsacum genes, for it showed some of the vegetative characters of Tripsacum.

In the later phases of the first division, from diakinesis to anaphase, numerous figures were found showing that the pairing was irregular in several chromosomes. In plant 46, a trivalent was frequently observed, but the Tripsacum chromosome was also found detached in a cell in which four pairs were associated. Plant 16 showed nine bivalents and a trivalent at diakinesis in most cells. At anaphase, cells were seen in which eleven approximately normal chromosomes were moving to one pole, and ten to the other. Still another condition was observed in which disjunction had occurred among the bivalents generally, but in the end of the cell towards which eleven chromosomes were moving, four of them were definitely in pairs (Fig. 67G). It is probable that in this cell, one or two quadrivalents had been formed in addition to a trivalent.

Longley (1937) reported a preliminary study of the chromosomes of *Tripsacum floridanum* and the diploid form of *T. dactyloides.* He stated that the study made up to the time of his report indicated that all of the chromosomes of Tripsacum have terminal knobs, making them more like the chromosomes of Euchlaena than Zea. Our own observations of the chromosomes of Tripsacum, made incidentally, also indicate numerous knobs. The Tripsacum chromosome involved in these trisomes, rings, and chains has never shown a knob, but the scheme shown in Figure 69 explains how both ends may be lost. In certain stocks of the hybrids under discussion, chromosome 10 often was found to have a sub-terminal knob. This is of interest in that Longley (1938), in a study of the chromosomes of many varieties of maize, found chromosome 10 always to be knobless except in abnormal cases. This immediately suggests that the knob found on chromosome 10 in our study may have been acquired from Tripsacum, for chromosome 10 always appeared to be otherwise normal.

Effects of the Extra Tripsacum Chromosome: Plants possessing the extra Tripsacum chromosome can usually, but not always, be distinguished from normal 2n plants in the same population. The leaves of the 2n + 1 plants are usually stiffer and more glossy, the stalks frequently slightly stunted.

A comparison of cross sections of the leaves of Zea, Tripsacum and 2n + 1 plants reveals several additional differences. The sheaths of the vascular bundles of Tripsacum (Fig. 70D) are distinctly more sclerotic than are those of Zea (Fig. 70A). This accounts for the higher degree of stiffness of the leaves of Tripsacum. The 2n+1 plants show a closer resemblance to Zea, but they are intermediate between the two parents (Fig. 70C). The hygroscopic cells are in larger groups in Tripsacum than in Zea, and the 2n + 1 plants are approximately like Zea in this respect. Table 20 shows that the rows of hygroscopic cells also are closer in Tripsacum than in Zea, and this abundance of hygroscopic cells in Tripsacum probably accounts for its greater resistance to drought. In distance between rows of hygroscopic cells, the 2n+1 plants are again intermediate between their parents. Zea and the 2n+1 plants usually have a row of stomates between each two vascular bundles, while in Tripsacum the rows of

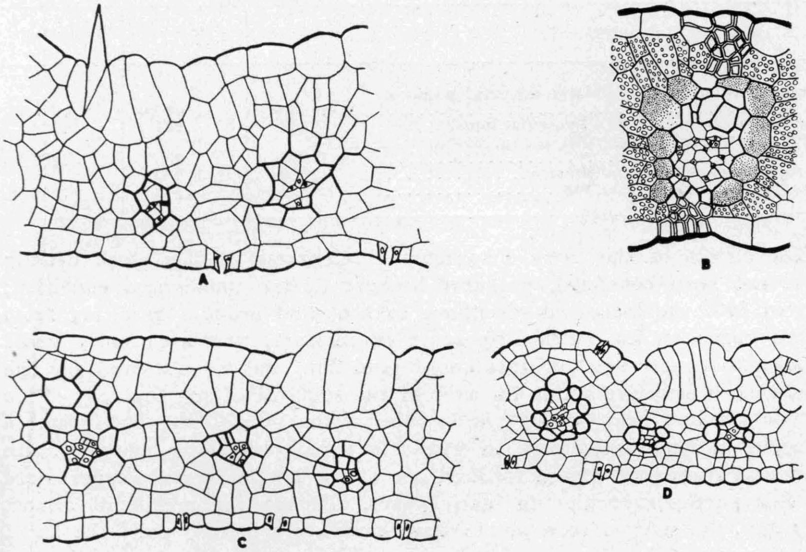

Fig. 70. Cross sections of leaves of *Zea mays*, *Tripsacum dactyloides*, and 2n+1 hybrid; X 74. A. Zea, showing representative portion. B. Zea, large vascular bundle. C. 2n+1 hybrid, representative portion. D. Tripsacum, representative portion.

stomates are irregularly distributed. There is a class of large vascular bundles, including the midrib, that often has rows of sclerotic cells, apparently tracheids, above and below, sometimes including the lower and upper epidermis (Fig. 70B). The 2n+1 plant is intermediate between its parents in distribution of these (Table 20, Fig. 72). There are two types of pubescence on both Zea and Tripsacum, one type being several times as long as the other. In Zea the hairs are mostly of the long type; in Tripsacum they are mostly of the short type; and in 2n+1 plants it is not easy to determine which type predominates. In some plants the first is most common, and in others the second. The vascular bundles of Tripsacum are extremely variable in size, while in Zea and the 2n+1 plants they are more uniform, although the 2n+1 type is apparently intermediate. Other anatomical data are given in Table 20.

Table 20. Anatomical measurements of the leaves of Zea, Tripsacum, and 2n+1 plants

Characters	Zea	2n +1	Tripsacum
Average distance apart of large vascular bundles, mm.	1.440	1.086	.293
Average distance apart of all vascular bundles, mm.	.142	.141	.084
Average distance between rows of hygroscopic cells, mm.	1.260	.955	.291
Average thickness of midrib, mm.	1.500	1.250	.850
Average thickness of leaf, mm.	.193	.142	.132

The effects of the extra Tripsacum chromosome in this stock usually have not been beneficial, probably because of the unbalanced condition; but in 1937 the increased resistance to heat and drought resulting from genes borne on the extra Tripsacum chromosome was apparently great enough to counteract the unbalanced condition, and we observed for the first time a selective action in favor of the survival of 2n+1 plants. This population had been planted quite late in the season, the last week in June, at a time when corn in Texas is usually reaching maturity. In July and August it passed through one of the hottest periods experienced in this particular region in many years. During the middle of almost any day, the normal corn plants were completely wilted, while the 2n+1 plants were still quite turgid. Many of the normal corn plants failed to survive this period, while few of the 2n+1 plants were lost. This increased resistance to heat and drought of the 2n+1 plants may be accounted for by the increased number of hygroscopic cells.

Discussion of Results from Zea x Tripsacum Hybrids

There are a number of very pertinent implications involved in the genetic and cytological results which have accrued from the studies of the various Zea x Tripsacum hybrids. That the two genera can be crossed at all speaks of a closer relationship than most botanists have assumed and suggests that Tripsacum must receive due consideration in any comprehensive study of the phylogeny of maize.

Another important consideration is the fact that although there is very little association between Zea and Tripsacum chromosomes in the F_1 hybrid, so little in fact that unreduced gametes are regularly formed, nevertheless some association does occur. Feeble pairing, presumably between Zea and Tripsacum chromosomes, is frequently observed at diakinesis in the F_1 hybrid, while in the triploid hybrid (Zea x Tripsacum) x Zea, trivalent associations to the number of four have been encountered. In the succeeding generation there is a great excess of plants with 0, 1, and 2 Tripsacum chromosomes, suggesting that two of the Tripsacum chromosomes have associated regularly with the Zea chromosomes and passed to the poles with one member of the pair. Cytological studies of $2n + 1$ plants, in which the extra Tripsacum chromosome bears an allele of the sugary gene in maize, show frequent association of this particular chromosome with chromosome 1 of Zea and occasional association with Zea chromosomes 4, 5, and 9. Formation of rings and chains indicates that interchange between the Tripsacum chromosome and various Zea chromosomes has occasionally occurred. In one case the starchy gene from Tripsacum has apparently been transferred to one of the Zea chromosomes. In another case other Tripsacum genes have been transferred, for we find a Tripsacum influence on plants lacking an extra Tripsacum chromosome. All of this evidence combined suggests strongly that Tripsacum germplasm can be transferred to Zea, and sometimes with beneficial results; for, as already mentioned, $2n+1$ plants survived better than normal corn plants under certain conditions in spite of the unbalance resulting from the extra Tripsacum chromosome.

All of these considerations compel us to ask the question: What would be the consequences if such a cross occurred in nature? We can no longer dismiss this question as Weatherwax (1935) has done, and as we previously were inclined to do, with the assumption that mechanical difficulties and the small number and low vitality of the seeds produced precludes any probability of the natural hybridization of these genera; for while our success was achieved only by producing thousands of opportunities for hybridization to occur, nature must have provided millions of opportunities over a period of hundreds of years.

If a hybrid of Zea and Tripsacum had ever occurred in nature, it would probably, like our hybrids, have produced seed only when crossed back to Zea or Tripsacum. In the next generation of the backcross to Zea, all of the plants would have had ten pairs of maize chromosomes with a varying number of extra Tripsacum chromosomes ranging from none to 18. The extra Tripsacum chromosomes, because they are not transmitted through the pollen, and because they result in an unbalanced condition, usually associated with a stunting of the plant, would have been rapidly eliminated, although under certain conditions $2n+1$ plants, because of their greater resistance to heat and drought, might have had a survival value. In the end, however, only pure corn plants, or corn plants with a few Tripsacum genes, resulting from an interchange between Zea and Tripsacum chromosomes, would have survived. The corn with a few

Tripsacum genes in its chromatin would have been able to survive in the wild only if those genes governed the expression of characters which ordinary corn now lacks and which are essential to its existence as a wild species. There may be many such characteristics but there are certainly two conspicuous ones; the first is protection for the seed, and the second is a means of dispersal. Tripsacum possesses, and theoretically could transmit to Zea, both of these characteristics, the first in the form of prominent horny glumes, the second in the form of a brittle rachis.

If we were to endow Zea with prominent horny glumes and a brittle, readily disarticulating rachis, we should have a plant very similar to one already in existence, namely Euchlaena, or teosinte. And thus this line of reasoning has led us to consider seriously for the first time, an unpublished suggestion by Dr. Edgar Anderson that teosinte is nothing more than the product of the natural hybridization of Zea and Tripsacum.

We had previously dismissed this suggestion as fantastic, and not until the summer of 1937, when we had convinced ourselves that exchange of chromatin between Zea and Tripsacum does occur, did we again consider it.

The historical development of this conception is given in some detail here because we believe that it is of importance to distinguish between the eight years of genetical and cytological studies which have preceded this hypothesis, and the various investigations which have followed it. For once a plausible hypothesis is developed, it is very difficult to remain completely unbiased, and the scientist seeking only the truth unconsciously becomes an advocate striving to prove his case.

Genetics of Euchlaena Hybrids

Our experiments with hybrids of maize and teosinte began before the work on the Zea x Tripsacum hybrids had been completed and were initiated primarily for the purpose of determining how the genes which differentiate the two genera, Zea and Euchlaena, are distributed on the chromosomes. Do they occur at random over all the chromosomes or are they concentrated only in certain ones? Are the genes for profuse tillering, for example, on the same chromosomes as the genes for number of tassel branches or are they on different ones?

These questions have arisen because there has always been, but more especially in the past, a common opinion among biologists, including a few geneticists, that Mendelian heredity involves only superficial characteristics, while the characteristics which differentiate genera and species are transmitted from generation to generation by another mechanism. This viewpoint is expressed in the picturesque language of Loeb (1919). "The egg," he states, "is the embryo in the rough carrying the genus—or even the species—heredity while Mendelian heredity adds only the finer details to the rough block." And again in the statement of Conklin (cf. Wilson 1928): "We are vertebrates because our mothers were vertebrates and produced eggs of the vertebrate pattern; but the color of our skins and hair and eyes, our sex, stature and mental peculiarities were determined by the sperm as well as by the egg from which we came."

A similar viewpoint finds its expression even among geneticists, for Castle (1933), in discussing the gene theory in relation to blending inheritance, says: "The chromosomes are the undoubted mechanism for the transmission of characters which follow Mendel's law in inheritance. But the more general features of organization are not so inherited. They follow a law described by Galton as blending inheritance. The cytoplasm of the egg-cell affords a suitable mechanism for the transmission of blending characters, although it must be recognized that genes borne in chromosomes may modify such characters," and again (1936) in discussing size inheritance in mice: "But on theoretical grounds, I, for one, am inclined to think that we may have gone too far in ascribing heredity exclusively to the action of genes borne on the chromosomes."

The attitude expressed in these quotations has become, in recent years, a minority one. Muller (1926) has expressed the opinion of the majority very concisely in his statement:

"It may be reiterated at this point that there is no good evidence from genetics of any heritable differences between organisms except such as are resident either in the numerous genes of the nuclear 'chromatin,' or, much more rarely, in the plastid primordia, which may contain a homologous substance. And since our evidence is extensive, and the phenomenon of heritability a highly peculiar one, it is logical to conclude that in all probability all specific, generic, and phyletic differences, of every order, between the highest and the lowest organisms, the most diverse metaphyta and metazoa, are ultimately referable to changes in these genes—chiefly in the multitudinous and very diverse chromosomal genes, to a lesser extent in the plastid genes."

Although most geneticists would agree with the viewpoint expressed by Muller, it must be admitted that the direct evidence in favor of this view is rather limited, and most of the evidence bearing on the question is of a circumstantial nature. Results of numerous species crosses have shown that most of the characters differentiating species involve multiple factor inheritance. The evidence that this type of inheritance is not essentially different from simple Mendelian inheritance has accumulated rapidly. In fact the theory of multiple factors has been definitely confirmed, except for the most skeptical, by the work of Warren (1924), Sax (1923, 1924), Sirks (1925), Lindstrom (1924, 1926a, b, 1927, 1929, 1931), and others who have demonstrated linkage between qualitative and quantitative genes.

Nevertheless there is not a single case, with the possible exception of Green's (1931, 1933) species crosses in mice,—and Castle (1932, 1936) questions some of the evidence presented here,—in which sufficient data have been accumulated to demonstrate that the differences between species or genera are governed by definite genes located in particular chromosomes.

It occurred to us that we had in hybrids of Zea and Euchlaena the best material, either among plants or animals, for obtaining conclusive evidence for the existence of "genus" and "species" genes in the chromatin. The two genera have the same chomosome number; they hybridize readily with each other (Figs. 71-73). There is almost complete pairing of the Zea and Euchlaena chromosomes in the hybrid (see p. 47), and the chromosomes of Zea cross-over with those of Euchlaena almost as readily as do the chromosomes in pure Zea. The hybrid is highly fertile and can be backcrossed readily to either parent. Finally the two genera differ decidedly in many characteristics which can be measured quantitatively; and what is of still greater importance, each of the ten maize chromosomes can be marked by two or more genes, the inheritance of which has already been determined.

One of the weaknesses involved in a number of earlier experiments on linkage of quantitative and qualitative characters has been the large number of chromosomes concerned and the relatively small differences which were studied. Castle (1933), for example, failed to find any indication of linkage of size genes with four color genes in crosses between large and small races of rabbits. Yet the average difference between the two races was so small and the chromosome number so large that it is not surprising that the results of Castle's experiments are negative (cf. Dobzhansky 1934).

The situation in the Zea x Euchlaena hybrids is quite different. Not only is the chromosome number relatively small, 10, but the differences to be studied are enormous. Euchlaena, for example, bears only five or six seeds in a single lateral pistillate spike, Zea several hundred to more than a thousand. Finally we are able to mark the chromosome not by one gene alone but by several. For example, we may cross a stock of maize having two marker genes, *B* for sun red color and *lg* for liguleless, which are 34 cross-over units apart on the second chromosome, with Euchlaena, which carries the alleles of both of these genes also on the second chromosome. When such a hybrid is crossed back to a double recessive maize stock *b lg* we obtain in the next generation four classes of plants, as follows: *B lg, B Lg, b lg, b Lg*. (Fig. 74.) The first and fourth class are the parental maize and teosinte classes, respectively, while the two middle classes are cross-overs.

It is evident that the plants exhibiting both of the genes received from maize, *B* and *lg*, except those few which are the result of double cross-overs, have received intact a section of the maize chromosome, at least as long, and probably slightly longer than, the distance between the two genes, while those which exhibit the genes *b* and *Lg* have received a corresponding section of chromatin from teostinte, except in the rare cases where double cross-overs have occurred.

Assuming that the genes which differentiate the two genera are numerous and are scattered more or less at random throughout the chromatin, then the *B lg* plants should, as a class, most resemble maize in their characteristics, while the *b Lg* plants as a class should most resemble teosinte with the two cross-over classes lying somewhere between these two extremes.

Fig. 71. First generation hybrid of maize X Florida teosinte.

It is, of course, obvious that any particular plant will approach in its characteristics one or the other of its parents, not as the result of genes borne on the one chromosome under investigation but as the result of genes borne on all of them. It is, however, equally obvious that if non-homologous chromosomes assort independently of each other, and there is no evidence to the contrary, then the plants in the red liguleless class should, on the average, receive the same number of Zea and Euchlaena genes as those of the green liguled class, *except* for such genes as reside on the second chromosome in the region lying between *B* and *lg*.

The chief weakness of this experiment, as of most studies on linkage of qualitative and quantitative factors, is that it is not always easy to distinguish between the direct effects of the marker genes themselves and the genes which are linked with them. For example, we know from years of observation that liguleless plants have, on the average, fewer tillers than normal liguled plants. We should expect, therefore, that the liguleless plants segregating from the Zea x Euchlaena hybrids would have fewer tillers than normal plants in the same progeny, even if there were no genes for tillering from the freely-tillering parent, Euchlaena, involved in the cross.

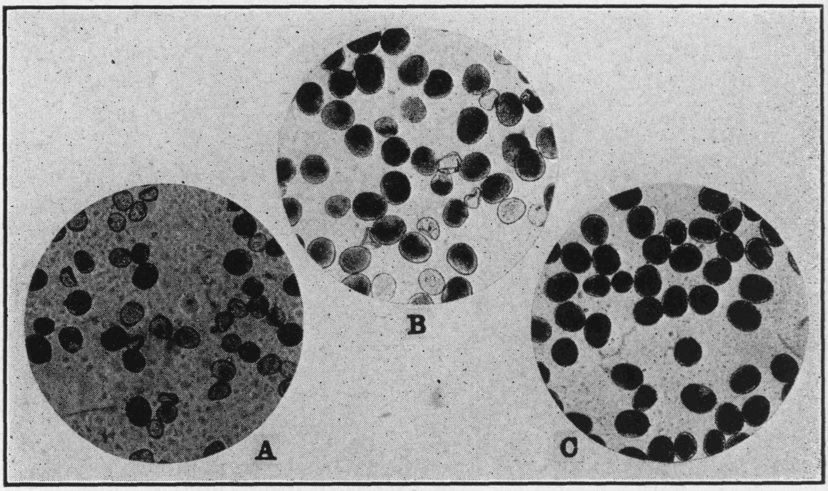

Fig. 72. Pollen of hybrids of A. Perennial teosinte X maize. B. Florida teosinte X maize and C. Durango teosinte X maize. The first produces a high proportion of aborted pollen, the second approximately 50 per cent of small and aborted pollen, while the third produces mainly normal pollen.

On the other hand, we also know that liguleless plants in pure maize are inclined to produce slightly smaller ears with slightly fewer seeds than normal plants. In the hybrid of Zea x Euchlaena, however, the gene for liguleless goes into the cross with genes from Zea for large ears and many seeds, in contrast to the genes from Euchlaena for small ears

Fig. 73. Lateral inflorescences of first generation hybrids of Florida teosinte X maize (*Tu tu*). The membranaceous glume of pod corn completely replaces the indurated shell of teosinte.

and few seeds. In this case, if the liguleless plants have fewer seeds than normal plants, we must attribute the differences to the direct effects of the liguleless gene in reducing the size of the ear. But if the liguleless plants have *more* seeds on the average than normal plants, we can only conclude that the liguleless gene has brought into the cross, closely associated with it on the same chromosome, a gene or genes for seed number with sufficient effect to more than counteract the direct effect of the liguleless gene itself.

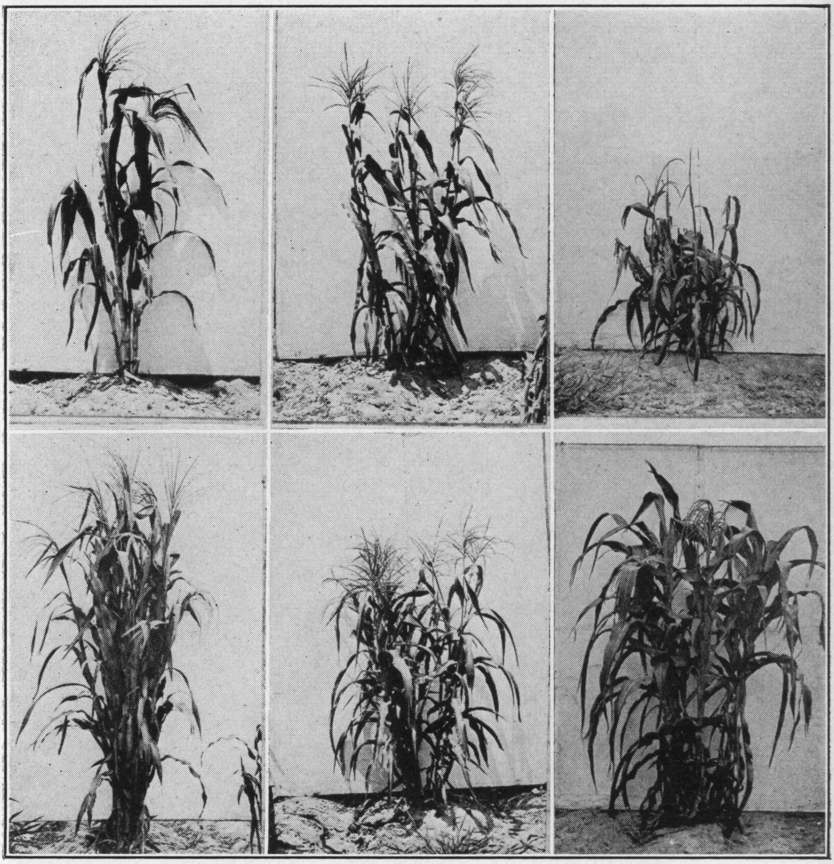

Fig. 74. Segregates from the cross Zea (*b lg*) X [Euchlaena (*b Lg*) X Zea (*B lg*)]. The various genotypes were compared in characteristics which differentiate Zea and Euchlaena to determine whether genes governing these characteristics were linked with genes for qualitative characters. (See Table 21.)

We have attempted, so far as this has been feasible, to confine the marker genes to those which are known from experience to have but little direct effect upon the characters being measured, and though this was not always possible we have at least avoided such genes as teopod, ramosa, and various dwarfs which have *per se* a decided effect upon some of the characteristics under consideration.

Among the characteristics measured or recorded were the following:

1. Number of days to anthesis: Recorded by tagging each plant on the day that the first anthers were exserted. Under Texas conditions corn planted on March 15 blooms late in May or early in June. Teosinte planted at the same time does not bloom until about October 15th.
2. Height of stalk: Measurement made in centimeters from the ground to the base of the tassel on the main stalk. Under Texas conditions of the stalks of Florida teosinte are usually taller than those of maize.
3. Height of tallest tiller: Measurement made in the same way as the preceding one. The tillers of maize except those of the profusely tillering Northern flint and flour corns are seldom as tall as the main stalk. In teosinte the tillers are often taller than the main stalk.
4. Number of tillers: Determined by actual count of the stalks arising at or below the surface of the ground. The maize stocks used in these crosses seldom exhibited more than one or two tillers. Teosinte usually has about fifteen.
5. Number of leaves, main stalk: Determined by actual count. There is but little difference in maize and teosinte in this characteristic.
6. Number of leaves, tiller stalks: Determined by actual count. There is a tremendous difference between maize and teosinte in this characteristic, a difference which is partly related to the difference in number of tillers.
7. Number of leaves, total: Obtained by adding the two preceding values.
8. Number of ears, main stalk: All pistillate inflorescences from which silks emerged were counted as ears. Maize usually bears not more than two or three; teosinte one or more at almost every node.
9. Number of ears, tiller stalks: Determined as in No. 8. Maize seldom has ears on the tiller stalks; teosinte always does when growth is normal.
10. Number of ears, total: Obtained by adding the two preceding values. The number of pistillate spikes in teosinte is usually several hundred and may exceed a thousand. The maximum number that we have seen in maize is eleven, and the number usually does not exceed three.
11. Number of ear branches: Both maize and teosinte develop secondary ears in the branches of the lateral inflorescences. In maize the secondary ears are usually latent unless the main ear is not pollinated. In teosinte the secondary ears usually develop on many of the lateral branches, and sometimes tertiary ears are produced. The number of ear branches represents the number of secondary and tertiary ears which appeared in the main lateral inflorescence of the main stalk.
12. Tassel branches, total: Determined by actual count of all branches, primary and secondary, in the terminal inflorescence of the main stalk.

Teosinte usually has a much larger number of tassel branches than ordinary maize.

13. Tassel branches, number, secondary: Most of the tassel branches of maize are primary; a large proportion of those of teosinte are secondary.

14. Tassel branches, per cent, secondary: The value obtained by dividing the preceding value by that of No. 12.

15. *Length of ears: Measured in centimeters, average of several ears* from each plant. The ears of maize are several times as long as those of teosinte.

16. Number of rows of grain: Teosinte is distichous; maize has many rows of grain, usually ranging from 8 to about 16 or 20. The spikelets of teosinte, however, are single, while those of maize are paired, so that the rows of spikelets in teosinte are two, in maize four to eight. In the backcross of the F_1 hybrid with maize all the ears were predominantly paired in their spikelets so that the number of rows of grain represents twice the number of rows of double spikelets. Counts were made on all ears harvested from each plant, usually three or four, and the results were averaged.

17. Number of ovules per row: Since the single spikelets of teosinte are alternate, there are seldom more than two or three in one row of the distichous inflorescence. Maize usually exhibits about 25 or 30, sometimes even more. Determined by averaging counts on several ears from each plant.

18. Total ovules per ear: An estimate arrived at by multiplying the number of ovules per row by the number of rows, and averaging the results from several ears of the same plant. Teosinte usually bears five or six ovules per ear, maize several hundred to more than a thousand.

It is obvious that many of the characteristics which we have measured are closely related to each other. Total number of ovules, for example, is wholly dependent upon the number of rows of grain and the number of ovules per row. Since we had no way of predicting in advance which of the measurements would express most accurately the differences between Zea and Euchlaena, we have included all of them in the tables.

Studies have now been completed with four chromosomes. The results are discussed in the following pages.

Florida Teosinte x *B lg* (Chromosome 2)

The total population from this backcross comprised 104 plants distributed as follows: *B lg*, 37; *B Lg*, 13; *b lg*, 28; *b Lg*, 26.

The two cross-over classes constitute 39 per cent of the total which does not differ significantly from the 34 per cent reported for maize, based on a summary including a total population of about 17,000 plants.* The results of the various measurements are set forth in Table 21.

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*All data for pure maize are taken from Emerson, Beadle, and Frazer (1935).

Table 21. Comparison, in characters which differentiate Zea and Euchlaena, of genotypes from the cross:
***b lg*(Zea) x [*b Lg*(Euchlaena) x *B lg*(Zea)]**

Character	Types compared		Diff.	P value	Types compared		Diff.	P value	Types compared			Diff. *B lg* — *b Lg*	P value
	B	*b*			*Lg*	*lg*			*B lg*	*B Lg* + *b lg*	*b Lg*		
No. days to anthesis	80.1	81.5	1.4	.30	81.4	80.6	.8	.60	79.5	81.6	81.4	1.9	.15
Height stalk, cm	148.6	148.6	0	.90	141.4	155.2	13.8*	.01	153.7	150.9	142.5	11.2	.07
No. tillers	3.3	4.8	1.5*	.01	4.5	3.9	.6	.15	3.2	4.2	4.9	1.7*	.01
No. leaves, main stalk	10.8	10.8	0	.94	10.7	10.9	.2	.35	10.8	10.9	10.7	.1	.70
No. leaves, tiller stalks	34.1	49.0	14.9*	.01	46.5	40.6	5.9	.15	34.0	42.8	50.7	16.7*	.01
No. leaves, total	44.9	59.9	15.0*	.01	57.2	51.5	5.7	.15	44.8	53.7	61.5	16.7*	.01
No. ears, main stalk	6.2	6.5	.3	.65	6.6	6.1	.5	.40	5.9	6.4	6.6	.7	.35
No. ears, tiller stalks	7.2	11.4	4.2*	.01	11.6	8.1	3.5*	.02	6.3	9.6	12.5	6.2*	.01
No. ears, total	13.4	17.8	4.4*	.02	18.2	14.2	4.0*	.03	12.2	16.0	19.1	6.9*	.01
Tassel branches, total No	23.0	23.3	.3	.85	26.2	20.4	5.8*	.01	22.1	20.7	26.7	4.6*	.03
Tassel branches, No. secondary	6.4	6.5	.1	.90	7.8	5.2	2.6*	.01	5.8	5.6	7.8	2.0	.10
Tassel branches, % secondary	26.4	25.1	1.3	.60	27.1	24.3	2.8	.20	24.9	25.5	26.2	1.3	.65
No. rows grain	7.6	7.7	.1	.90	7.5	7.8	.3	.30	7.7	7.8	7.5	.2	.70
No. ovules per ear	136.0	140.9	4.9	.70	122.1	154.8	32.7	.02	143.0	151.9	122.1	20.9	.25
Total No. plants	50	54	....	....	39	65	....	....	37	41	26	....	....

*Significant difference may be due to direct effects of marker genes.

Significant differences are shown between red and green plants in number of tillers, number of tiller leaves, total number of leaves, number of tiller ears, and total number of ears. These differences are all in favor of the green plants and might indicate that the recessive *b* factor has brought into the cross some genes from Euchlaena governing these characteristics. It has frequently been observed in pure maize, though never verified by adequate data, that red plants show less tendency to tiller than green plants in the same population. The differences in this cross may be nothing more than a manifestation of this tendency.

The comparison of normal and liguleless plants shows significant differences in height of stalk, number of tiller ears, total number of ears, total number of tassel branches, number of secondary tassel branches, and number of ovules. All of these differences, except that involving number of ovules, can be accounted for as direct effects of the liguleless gene.

The final comparison of the two parental combinations with each other and with the cross-overs shows significant differences between the parental classes in number of tillers, number of leaves of the tiller stalks, total number of leaves, number of ears on the tiller stalks, total number of ears, and total number of tassel branches. All of these differences are already accounted for as possible effects of the marker genes, so that there is no conclusive evidence of linkage of the marker genes with other genes which differentiate the two parental genera, so far as these particular characteristics are concerned.

Florida Teosinte x *wx* (Chromosome 9)

Only one gene, waxy, was used as a marker for the ninth chromosome because previous work by Emerson and Beadle (1932) and Beadle (1932 a, b) had shown that the waxy gene resides in a region that does not pair regularly with its maize homolog and shows but little crossing-over with it. Beadle's studies indicate that this region is the equivalent of approximately 45 cross-over units.

A total population of 279 plants was matured, of which 155 had originated from non-waxy and 124 from waxy seeds.

The comparison of plants from waxy and non-waxy seeds is shown in Table 22.

Significant differences are found in height of stalk, number of tillers, number of leaves on the main stalk, number of leaves on the tiller stalks, total number of leaves, and total ovules per ear. All of these differences are in the direction expected as the result of linkage of the waxy gene with genes differentiating the two genera; none of them can be adequately accounted for as the effects of the waxy gene, although waxy plants are sometimes slightly weaker than plants from non-waxy seeds and the first four differences may be a consequence of this, though the last one could not be. We have in this cross, then, an indication of linkage. It is rather surprising, however, to find so few significant differences and to find that those which are statistically significant are still quite small. The chro-

Table 22. Comparison, in characters which differentiate Zea and Euchlaene, of genotypes from the cross, *wx*(Zea) x [*Wx*(Euchlaena) x *wx*(Zea)]

Character	Types compared		Diff.	P value
	Wx	*wx*		
No. days to anthesis	73.6	72.7	.9	.30
Height stalk, cm	155.8	148.7	7.1*	.05
Height tallest tiller, cm	142.3	147.8	5.5	.30
No. tillers	1.3	1.0	.3*	.01
No. leaves, main stalk	12.4	12.0	.4*	.05
No. leaves, tiller stalks	14.0	10.6	3.4*	.03
No. leaves, total	26.4	22.4	4.0*	.01
No. ears, main stalk	20.4	18.4	2.0	.10
No. ears, tiller stalks	6.4	5.6	.8	.60
No. ears, total	26.8	24.2	2.6	.15
No. ear branches	4.5	4.6	.1	.80
Tassel branches, total	31.6	32.2	.6	.50
Tassel branches, No. secondary	11.9	12.9	1.0	.10
Tassel branches, % secondary	37.7	40.1	2.4	.20
Length ears, cm	9.3	9.6	.3	.07
No. rows grain	8.1	8.3	.2	.25
No. ovules per row	19.2	19.4	.2	.80
Total ovules per ear	160.2	172.2	12.0	.02
Total No. plants	155	124	....	....

*Significant difference may be due to direct effects of marker gene.

mosome region involved in this cross is longer than that in any other cross studied and the question of double cross-overs is eliminated. We had anticipated larger and more numerous differences from this cross than any other, and the fact that they failed to occur indicates that the ninth chromosome carries fewer or less effective genes governing the expression of the characteristics under study than do some of the others.

Florida Teosinte x *Y Pl* (Chromosome 6)

A total of 211 plants of this cross reached maturity, distributed as follows: *Y Pl*, 60; *Y pl*, 39; *y Pl*, 47; *y pl*, 65.

The percentage of cross-overs is 41, which is considerably higher than the 28 per cent shown in the summary of all tests in maize. This may be due to errors in classification of the white and yellow seeds, which were very difficult to distinguish; or it may be no more than a random fluctuation. Anderson (cf. Emerson *et al* 1935) reports a cross-over percentage of 38 per cent for a population of 216 plants and this does not differ significantly from the percentage which we obtained in the teosinte cross.

The comparisons of the different classes of plants are shown in Table 23.

Plants from yellow and white seeds, respectively, differ significantly in total number of tassel branches, number of secondary tassel branches, and per cent of secondary tassel branches. All of these differences are in the direction expected as the result of linkage of the recessive *y* gene with genes for profuse branching of the tassel, introduced into the cross from teosinte. These differences cannot be attributed to the marker gene, because this gene has no noticeable effect upon any characteristic except color of endosperm.

Table 23. Comparison, in characters which differentiate Zea and Euchlaena, of genotypes from the cross:
***y pl* (Zea) x [*y pl* (Euchlaena) x *Y Pl* (Zea)]**

Character	Types compared		Diff.	P value	Types compared		Diff.	P value	Types compared			Diff. *Y Pl* — *y pl*	P value
	Y	*y*			*Pl*	*pl*			*Y Pl*	*Y pl* + *y Pl*	*y pl*		
No. days to anthesis	78.8	79.7	.9	.40	79.2	79.4	.2	.90	78.6	79.6	79.5	.9	.40
Height stalk, cm	92.7	100.2	7.5	.10	94.2	99.2	5.0	.25	91.0	96.8	101.6	10.6	.08
No. leaves, main stalk	10.6	10.6	0	.99	10.6	10.6	0	.99	10.6	10.5	10.6	0	.99
No. ears, main stalk	5.9	6.3	.4	.65	5.5	6.7	1.2	.10	5.1	6.6	6.4	1.3	.11
No. ear branches	2.2	2.3	.1	.65	2.0	2.5	.5	.18	1.8	2.5	2.3	.5	.30
Tassel branches, total	13.8	16.1	2.3	.01	14.4	15.6	1.2	.15	12.8	15.8	15.9	3.1	.01
Tassel branches, No. secondary	2.9	4.1	1.2	.01	3.4	3.7	.3	.60	2.5	4.0	3.8	1.3	.03
Tassel branches, % secondary	21.1	25.5	4.4	.01	23.6	23.7	.1	.90	19.5	25.3	23.9	4.4	.02
Length ears, cm	8.6	8.5	.1	.95	8.4	8.7	.3	.40	8.3	8.7	8.6	.3	.50
No. rows grain	7.8	7.7	.1	.90	7.6	7.9	.3	.30	7.6	7.8	7.8	.2	.50
No. ovules per row	19.3	19.5	.2	.90	19.0	19.8	.8	.45	18.4	20.2	19.2	.8	.60
Total ovules per ear	148.5	154.7	6.2	.60	148.6	155.1	6.5	.50	143.3	155.7	154.2	10.9	.40
Total No. plants	99	112	....	....	107	104	....	....	60	86	65	....	....

There is not a single significant difference between the purple and green plants in any of the characters studied.

A comparison of the two parental combinations *Y Pl* and *y pl* shows significant differences in the same three characteristics in which differences occurred between yellow and white. The differences, however, are in two cases slightly larger, indicating that there are included some genes for profuse tassel branching located in the region lying between *Y* and *Pl*.

Florida Teosinte x *su Tu* (Chromosome 4)

This cross, though it is the second to be studied, is discussed last because it differs so strikingly from the others. It comprised a total of 378 plants distributed as follows: *su Tu*, 44; *su tu*, 17; *Su Tu*, 96; *Su tu*, 221.

It is at once apparent that there is a great excess of normal and a deficiency of tunicate plants, as well as an excess of starchy and a deficiency of sugary. These same deviations had previously occurred in crosses of maize x Durango teosinte reported by Emerson and Beadle (1932).

The percentage of crossing-over between *su* and *Tu*, 29.9 per cent, is not, however, significantly different from the 29 per cent reported in the summary of linkage data, based on a total population of more than 18,000.

The results of comparing the different classes with respect to all characteristics measured, are shown in Table 24.

Plants from starchy and sugary seeds differ significantly in all of the measurements except number of days to anthesis and height of stalk. All of the differences are in the direction expected if the sugary gene is linked with genes which differentiate Zea from Euchlaena. Furthermore, most of the differences cannot be adequately accounted for as direct effects of the *su* gene *per se*, although plants originating from sugary seeds are inclined to be somewhat weaker than plants from starchy seed and it may be that the first nine differences are partly due to this.

A comparison of the tunicate and normal segregates shows significant differences in height of stalk, height of tallest tiller, number of ears on the main stalk, number of ears on the tiller stalk, total number of ears, total number of ear branches, length of ears, number of rows of ovules, number of ovules per row, and total ovules per ear. All of these differences are in the direction expected as the result of linkage, and none can be considered as direct effects of the marker gene.

A comparison of the parental combinations *su Tu* and *Su tu* shows significant differences in all characters except number of days to anthesis, number of tillers, number of leaves on the main stalk, number of tassel branches on tiller stalk, and total tassel branches. All of the differences are in the direction of linkage and none can be completely accounted for as direct effects of the marker genes.

At first glance it might be assumed that this cross shows a greater number of significant differences than do the other crosses only because the population is a larger one. Further consideration will show, however, that some of the differences, particularly those affecting ear characters,

Table 24. Comparison, in characters which differentiate Zea and Euchlaena, of genotypes from the cross: *su tu* (**Zea**) **x** [*Su tu* (**Euchlaena**) **x** *su Tu* (**Zea**)]

Character	Types compared		Diff.	P value	Types compared		Diff.	P value	Types compared			Diff. *Su tu*—*su Tu*	P value
	Su	*su*			*Tu*	*tu*			*Su tu*	*Su Tu* + *su tu*	*su Tu*		
No. days to anthesis	79.1	79.6	.5	.65	79.2	79.3	.1	.90	78.8	80.6	78.0	.8	.60
Height stalk, cm	171.7	167.2	4.5	.15	159.6	172.0	12.4	<.01	173.0	167.6	161.4	11.6	.01
Height tallest tiller, cm	154.3	135.5	18.8*	<.01	130.0	151.6	21.4	<.01	154.8	142.0	125.8	29.0	<.01
No. tillers	1.5	1.0	.5*	<.01	1.2	1.3	.1	.40	1.5	.9	1.3	.2	.30
No. leaves, main stalk	13.8	13.5	.3*	.02	13.6	13.7	.1	.60	13.9	13.4	13.6	.3	.40
No. leaves, tiller stalks	19.2	12.5	6.7*	<.01	15.1	17.1	2.0	.30	19.7	11.1	16.1	3.6	.15
No. leaves, total	33.0	26.0	7.0*	<.01	27.7	30.9	3.2	.15	33.6	24.9	28.6	5.0	.08
No. ears, main stalk	9.1	7.5	1.6*	.01	6.4	8.9	2.5	<.01	9.3	7.8	6.5	2.8	.01
No. ears, tiller stalks	3.0	1.7	1.3*	<.01	1.6	2.7	1.1	.05	3.1	1.9	1.5	1.6	.01
No. ears, total	13.0	11.1	1.9*	.02	7.9	13.1	5.2	<.01	13.3	12.0	7.8	5.5	<.01
No. ear branches	2.4	1.9	.5*	<.01	1.5	2.4	.9	<.01	2.5	2.2	1.4	1.1	<.01
Tassel branches, total	32.4	30.3	2.1	.05	32.3	31.4	.9	.50	32.5	29.3	33.5	1.0	.60
Tassel branches, No. secondary	12.8	10.6	2.2	<.01	12.2	11.9	.3	.80	12.7	10.5	11.9	.8	<.01
Tassel branches, % secondary	39.5	35.0	4.5	.03	37.8	37.9	.1	.80	39.1	35.8	35.5	3.6	.05
Length ears, cm	9.9	11.5	1.6	<.01	13.9	9.8	4.1	<.01	9.8	10.2	14.5	4.7	<.01
No. rows grain	8.3	9.1	.8	<.01	9.8	8.3	1.5	<.01	8.2	8.7	10.0	1.8	<.01
No. ovules per row	20.9	22.1	1.2	.02	23.6	20.9	2.7	<.01	20.9	20.9	24.5	3.6	<.01
Total ovules per ear	176.7	201.7	25.0	<.01	224.1	177.7	46.4	<.01	174.5	189.1	230.9	56.4	<.01
Total No. plants	238	140	....	....	61	317	....	....	221	113	44	....	....

*Significant difference may be due to direct effects of marker genes.

are much greater than those in other crosses, indicating that the fourth chromosome does bear more genes, or more effective genes, governing these characters than do chromosomes 2, 6, or 9.

In the light of these results it is interesting to re-examine Kempton's (1924a) experiments in this same field. These differ from ours in having only one marker gene on each chromosome, in using F_2 populations rather than backcross populations, and finally, in the use of Mendelian characters which have many effects. Kempton used three recessive characters—crinkly, ramose, and brachytic—the genes for which are located on chromosomes now designated as 3, 7, and 1, respectively. In every cross there are many significant differences between normal and recessive plants in the characters which differentiate maize and teosinte. However, when we eliminate those which may be the result of direct effects of the marker genes and also those which are in the wrong direction to indicate linkage, we find that in the crinkly cross only five differences remain: number of double female alicoles, number of single female alicoles, alicole index, days to pollen, and days to silk; and in the ramose cross only two differences remain: days to pollen, and days to silk. In the brachytic cross, however, there are eight significant differences which cannot be entirely attributed to the effects of the marker gene. These are: rows in terminal spike, position of best spike, length of best spike, number of rows of alicoles, number of single alicoles, alicole index, and days to pollen.

Considering Kempton's results with our own, we now have tests for linkage of qualitative and quantitative factors on seven of the ten chromosomes. In only two or three of these, the first and fourth, and possibly the third, is there clear-cut and convincing evidence of linkage between the marker genes and genes governing the expression of any large number of the characters which differentiate maize and teosinte.

Apparently the genes which differentiate these two genera are not distributed at random throughout all the chromosomes but are concentrated on a few particular chromosomes. Evidence presented later indicates that this is indeed the situation. The results, however, are quite conclusive in demonstrating that at least part of the differences which distinguish the two genera, Zea and Euchlaena, are due to genes which are borne on certain chromosomes and which exhibit linkage with the genes for simple Mendelian characters. Thus in spite of the surprising fact that several of the chromosomes tested have shown no clear-cut evidence of bearing genes which distinguish the two genera, we may still answer in the affirmative, at least so far as Zea and Euchlaena are concerned, the question, "Are differences between species and genera Mendelian?"

Reclassification of the Ears from Crosses of Zea and Euchlaena

The studies of linkage between quantitative and qualitative genes, described in the preceding pages, were made in the years 1932-1934. We had not intended to publish the results until similar studies on the remaining six chromosomes had been completed and this additional work had to be delayed while we developed appropriate tester stocks, adapted to Texas conditions, which carried two or more marker genes on each of the remaining chromosomes. In the meantime, however, the studies of hybrids of Zea and Tripsacum had brought forth evidence supporting the suggestion that Euchlaena may be nothing more than maize with a relatively small amount of Tripsacum chromatin superimposed upon, or substituted for, the maize chromatin. This suggestion led to a complete reversal of our approach to the problem of Zea-Euchlaena hybrids. We had assumed previously that Euchlaena was, as the taxonomists had classified it, a good genus, differing from Zea in many characteristics and by wide extremes. We had also assumed that these great differences must be governed by numerous genes, scattered more or less at random over the chromosomes.

But if Euchlaena differs from Zea by hundreds or thousands of genes, it would seem impossible, with the limited amount of chromatin exchange which occurs in hybrids of Zea and Tripsacum, for enough genes to be transferred from the latter to the former to produce Euchlaena.

We finally came to realize, however, that we had been considering all of the differences which distinguish Zea and Euchlaena instead of confining ourselves to the essential ones. If Euchlaena is nothing more than maize contaminated with a small amount of Tripsacum germplasm, then the original maize variety which entered into the cross was probably quite different from the North American varieties of today. For example, maize and Euchlaena differ quite markedly in number of tillers, our common varieties having few or none, and Florida teosinte about fifteen. Yet there are varieties of corn with almost as many tillers as Florida teosinte, and the freely-tillering characteristics of Euchlaena may have come, not from Tripsacum but from the particular variety of maize that crossed with Tripsacum to produce Euchlaena. Another striking difference between corn and Euchlaena is in time of maturity. Maize planted in Texas in March matures in about 130 to 140 days; Florida teosinte planted at the same time matures in about 250 days, a very wide difference. But there are varieties of corn in Colombia which require more than 300 days to reach maturity. Euchlaena might, therefore, have received its lateness either from corn or from Tripsacum.

When we exclude from consideration all differences between Zea and Euchlaena which are not fundamental and consider only the essential differences between the two genera, which are also important differences between Zea and Tripsacum, we find that there are four:

Paired pistillate spikelets vs. single pistillate spikelets.
Inconspicuous membranaceous glumes vs. prominent horny glumes.
Polytichous arrangement of spikelets vs. distichous arrangement.
Solid rachis vs. brittle rachis.

Fortunately, we had retained all the ears from our previous Zea-Euchlaena crosses in which we had been studying linkage of quantitative and qualitative characters. We re-examined this material in an attempt to classify it on the basis of the essential differences between Zea and Euchlaena, ignoring all other characters just as we would ignore them if we were, for example, studying the inheritance of sugary endosperm in a cross of an early, small-eared sweet corn with a tall, late, large-eared field corn.

It soon became apparent that one of these differences, paired vs. single spikelets, could not be studied in the material which we had available because the paired condition is dominant or nearly so; and when the F_1 hybrid is crossed back to Zea, the dominant parent with respect to this characteristic, all of the ears showed partial or complete pairing of the spikelets.

In studying the remaining characteristics—number of rows of spikelets, development of the glumes, and brittleness of the rachis—two facts became apparent: first that there were various degrees of development of these three characters; and second, that the characters were associated, a maximum development of the glumes being accompanied by a maximum reduction in the number of rows of spikelets, and both in turn correlated with an increased brittleness of the rachis. It was also evident that several factors were involved in the development of the glumes; for some ears had horny black glumes, others horny buff-colored glumes, and still others rather soft, colorless glumes.

It was also noted that certain types of ears were repeatedly encountered. One was a short, tapering ear with irregular rows, large seeds, and some staminate flowers at the tip of the ear. Another was a long cylindrical ear with straight rows, exhibiting a high percentage of sterility; but there were still others that failed to fit into either of these categories. Repeated attempts to arrive at a basis of classification resulted only in confusion; but they did bring out the fact that maize-like ears exhibiting none of the essential characteristics of Euchlaena were occurring about once in sixteen times, and ears resembling the F_1 hybrid were also occurring in approximately the same ratio. The frequent reappearance of the parental combinations suggested that either a small number of unit characters was involved or the parental combinations were reappearing more frequently than would be expected from chance assortment, as is often the case in species hybrids. However, the fact that the ordinary Mendelian characters of maize usually segregate in simple Mendelian ratios from maize-teosinte crosses in the same way as they segregate in pure maize crosses, seemed to preclude the possibility of a selective elimination of gametes in favor of the parental combinations, and pointed strongly to the fact that only a few factors, probably not more than four, were involved.

If this is the case, Collins and Kempton should have obtained maize-like plants or teosinte-like plants in the F_2 of their cross of corn and teosinte upon which they reported in 1920. If only four factors are involved, these parental combinations are each expected to occur once in 256 times, and one or the other of them once in 128 times.

In re-examining this paper we discover that from a population of 127 plants, Collins and Kempton reported and illustrated one teosinte-like plant which possesses the four essential characteristics of Euchlaena. A later paper by Kempton (1924a) on crosses of ramose and brachytic maize with teosinte illustrates one teosinte-like ear from a population of 119 in the first mentioned cross, and two teosinte-like ears from a population of 290 in the second cross. There may have been others not illustrated but at least this number occurred. Combining all these previously reported data, we find that the parental combinations have occurred at least four times in a total population of 536 plants. This represents a rate of 1:133, which is quite close to the theoretical ratio of 1:127 on the basis of four-factor segregation. It is true that these four parental combinations were all teosinte-like and none were maize-like; but since the chances of either occurring are equal, the odds against all of them being one type are only fifteen to one.

These published data do not, of course, verify a four-factor hypothesis, but they do suggest very strongly that only a relatively few factors are involved. If five were involved the parental combinations would be expected only once in 512 times instead of once in 128 times.

On the assumption that only four factors were involved, our populations resulting from the backcross to maize of the F_1 of teosinte and maize should fall in five main classes as follows:

Description	No. teosinte factors	No. each class
Resembling maize	0	1
Approaching maize	1	4
Intermediate	2	6
Approaching F_1	3	4
Resembling F_1	4	1

The first and last classes had already been observed, and in fact it was their relatively frequent occurrence which suggested that only a few factors were involved. These two classes were easily identified. A classification of the remaining ears into three distinct classes, one approaching maize, the second approaching the F_1 hybrid, and the third intermediate, presented no great difficulties; the ears fell into one or another of these three classes with very few exceptions that presented any doubt.

The first cross to be classified in this way, Euchlaena x *B lg*, gave the following results: Class 1, 3; Class 2, 30; Class 3, 50; Class 4, 27; Class 5, 7. If we assume that the classification is a sound one, the second class in this population should comprise four types, representing each of the unit characters. A type which had been repeatedly noted and which is characterized by a short tapering ear and the presence of staminate flowers at the tip, has already been mentioned. These were sorted out and found to comprise 10 of the 30 ears. A second type with large cylindrical ears, straight rows, and horny glumes pigmented with black was sorted out and found to comprise 6 of the 30 ears. This left 15 ears which were quite similar in appearance. It was discovered that part of these ears had horny glumes with a decided buff-colored pigmentation, while the remainder had softer glumes with no pigmentation. Separated on this basis, eight fell in the former class and six in the latter. When these separations had been completed it was apparent that there was a surprising resemblance between the ears within each group and many distinctions which had previously gone unnoticed between the different groups.

In describing and discussing these groups it seems desirable to designate them by literal symbols. There are two reasons for suspecting that the effects which differentiate the various groups are not due to single genes but to segments of chromatin which are usually inherited intact and to this extent behave as single genes. One reason for believing this is the fact that several ears have been found which cannot be classified as pure maize; they show some of the characteristics of one of the four distinctive groups, but do not show all of them. These ears can be explained as representing the presence of part of one of the segments, but not all of it. Since single genes could not be expected to break up in this fashion, but short segments of chromatin would naturally do so occasionally, it has been assumed that each of the so-called factors represents a group of genes rather than a single one. Other evidence in favor of this view comes from a cross of maize and Durango teosinte. In this population the ears can be classified into the same groups, but the four groups in the second class show fewer differences between each other and less difference from pure maize than they do in the crosses in which Florida teosinte is one parent. This indicates again that either the gene has split, losing part of its effect, or the chromatin segment has become shorter, losing part of its genes. The latter explanation is the more plausible one and we are tentatively assuming that each of these four factors is in reality a short segment of chromatin which, because it exhibits Tripsacum effects, probably was received originally, by some form of segmental interchange, perhaps translocation, from Tripsacum. In conformity with the terminology adopted by maize geneticists, these segments are designated as translocation segments* T-A, T-B, T-C, T-D, while the different primary types which result from them are called A type, B type, etc.

The four primary types may be described as follows:

A type: Long, slender ear, cylindrical in shape, with straight rows of grain which are distinctly divided in pairs; glumes prominent, horny, with black pigment; seed intermediate in size and shape, many failing to develop. No staminate flowers.

B type: Short, plump, tapering ears, with irregular rows; glumes soft and colorless; seed large and round; ears well-filled and always bearing staminate flowers at the tip.

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*This use of the term may not be strictly accurate for it is possible that the transfer of chromatin occurred as the result of crossing-over between partially homologous chromosomes. (See p. 161.)

C type: Long cylindrical ears intermediate in diameter, with straight rows of grains; glumes prominent, horny and buff-colored; seeds small and often decidedly pointed; ears poorly filled; staminate flowers usually absent. This class resembles A but differs from it in having buff-colored glumes instead of black.

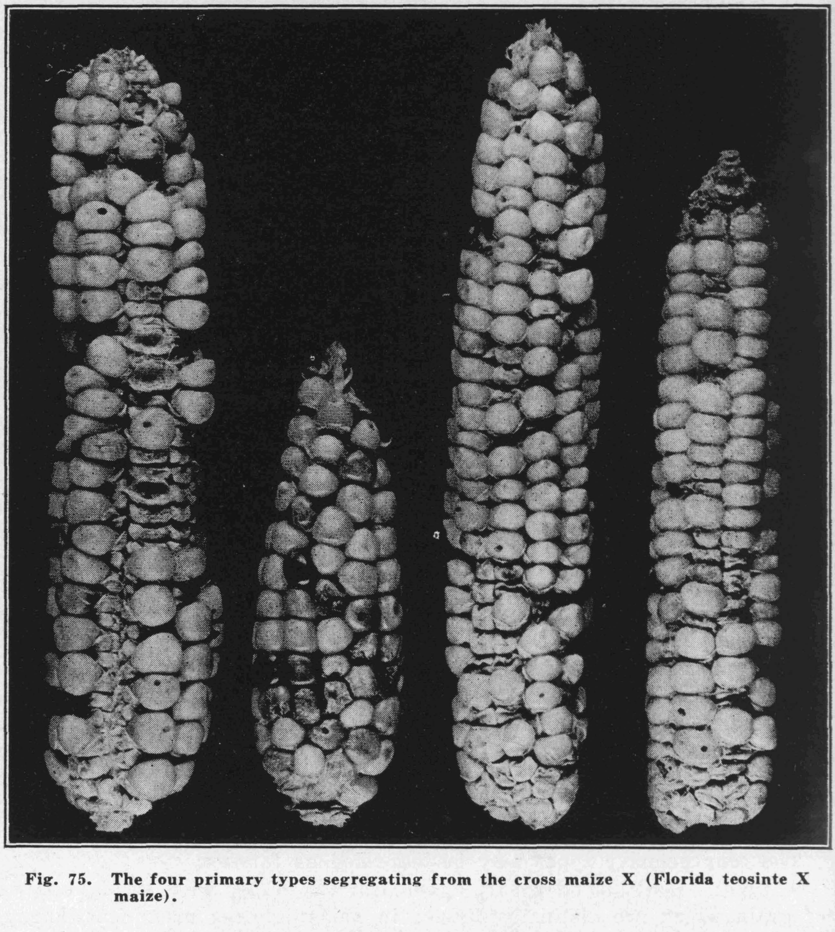

Fig. 75. The four primary types segregating from the cross maize X (Florida teosinte X maize).

D type: Ears intermediate in length and diameter, cylindrical in shape, usually straight rows but not so well defined as in A and C. Well filled, seeds large and round; glumes soft and colorless; staminate flowers few or absent. Resembles B in many characteristics but is quite different in size and shape of ear.

Ears of each of these classes are illustrated in Fig. 75.

After these four classes had been successfully separated and described, it was possible to separate the six types with two segments, AB, AC, AD, BC, BD, and CD, and the four types with three segments, ABC, ABD, ACD and BCD, with the results shown in Tables 25 and 26. Fig. 76.

The ears in this population may be classified in still another way, lacking A or having A, lacking B or having B, etc. In each of these four classifications the two classes are expected to occur in equal numbers. The numerical results are shown in Table 27.

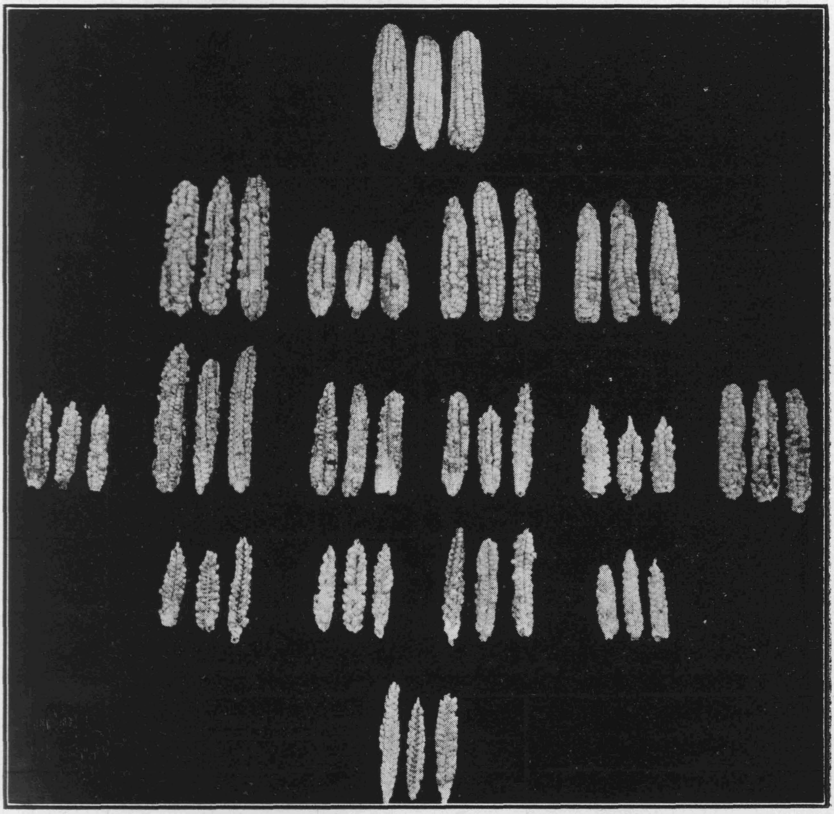

Fig. 76. **Selected sample of three ears each of 16 classes occurring in the cross maize X (Florida teosinte X maize). The upper three ears are essentially maize; the lower ears practically duplicate the F_1 hybrid.**

In both classifications, the summary of all data shows deviations from the theoretical numbers too great to be attributed to chance fluctuations. Part of these deviations are undoubtedly the result of errors in classification. That some of these occurred there can be no doubt. But part of the deviation is also due to a marked excess of the A and C classes. There was an excess of A plants in three of the four crosses and an excess of C in all of them. The deviation was especially great in the teosinte-*su Tu* cross, although both B and D occurred in expected numbers in this cross.

The next step is to determine whether there is linkage between these four translocation segments A, B, C, and D, and the genes which had been used to mark the various chromosomes. This determination is purely an objective one, for all of the classifications with respect to the Mendelian characters involved had been made three, four, and five years previously and the data were not again consulted until the new classification on the basis of translocation segments had been completed. The tests for linkage are shown in Tables 28 to 32.

Table 25. Distribution of plants in sixteen theoretical genotypes resulting from independent inheritance of four translocation segments

T– Segments present	No. plants each cross				Total No.
	B lg	*wx*	*Y Pl*	*su Tu*	
None	3	12	0	7	22
A	6	18	5	22	51
B	10	15	6	10	41
C	8	14	6	40	68
D	6	11	4	9	30
AB	8	18	11	43	80
AC	10	26	13	50	99
AD	7	13	7	31	58
BC	9	17	6	15	47
BD	8	13	7	19	47
CD	8	17	9	19	53
ABC	9	27	19	30	85
ABD	7	22	27	23	79
ACD	4	24	23	23	74
BCD	7	20	18	20	65
ABCD	7	6	2	6	21
Total	117	273	163	367	920
P value	.95	.02	<.01	<.01	<.01

Table 26. Distribution of plants according to number of translocation segments

No. segments	No. plants each cross				Total No.
	B lg	*wx*	*Y Pl*	*su Tu*	
0	3	12	0	7	22
1	30	58	21	81	190
2	50	104	53	177	384
3	27	93	87	96	303
4	7	6	2	6	21
Total	117	273	163	367	920
P value	.95	<.01	<.01	<.01	<.01

Table 27. Distribution of plants according to presence or absence of different translocation segments

Translocation segments	Cross	No. of plants		Theor. present	P value
		Translocation segments			
		Present	Absent		
A	*B lg*	58	59	58.5	.50
A	*wx*	154	119	136.5	.03
A	*Y Pl*	107	56	81.5	<.01
A	*su Tu*	228	165	196.5	<.01
Total		547	399	473	<.01
B	*B lg*	65	52	58.5	.02
B	*wx*	138	135	136.5	>.50
B	*Y Pl*	96	67	81.5	.02
B	*su Tu*	166	163	164.5	>.50
Total		465	417	441	.10
C	*B lg*	62	55	58.5	.20
C	*wx*	151	122	136.5	.08
C	*Y Pl*	96	67	81.5	.02
C	*su Tu*	203	190	196.5	.50
Total		512	434	473	.01
D	*B lg*	54	63	58.5	.09
D	*wx*	126	147	136.5	.20
D	*Y Pl*	97	66	81.5	.02
D	*su Tu*	150	179	164.5	.10
Total		427	455	441	.34

Table 28. Recombinations in the cross:

$$b\ lg\ \textbf{t-a t-b t-c t-d (Zea) x}\ \frac{+\ +\ \textbf{T-A T-B T-C T-D (Euchlaena)}}{B\ lg\ \ +\ \ +\ \ +\ \ +\ \ \textbf{(Zea)}}$$

Genes XY	Linkage phase	No. of plants				Recombinations		P value
		XY	*Xy*	*xY*	*xy*	No.	Per cent	
B Lg	R	14	24	43	36	50	43	.14
B T-A	R	16	42	22	37	53	45	.28
B T-B	R	22	43	16	36	58	50	.50
B T-C	R	17	45	21	34	51	44	.20
B T-D	R	14	40	24	39	53	45	.28
Lg T-A	C	25	33	32	27	65	56	.20
Lg T-B	C	38	27	19	33	46	39	.02
Lg T-C	C	31	31	26	29	57	49	.50
Lg T-D	C	31	23	26	37	49	42	.08
T-A T-B	C	31	27	34	25	61	52	>.50
T-A T-C	C	30	28	32	27	60	51	>.50
T-A T-D	C	25	33	29	30	62	53	>.50
T-B T-C	C	32	33	30	22	63	54	.38
T-B T-D	C	29	36	25	27	61	52	>.50
T-C T-D	C	26	36	28	27	64	55	.28

Table 29. Recombinations in the cross:

$$wx\ \textbf{t-a t-b t-c t-d (Zea) x}\ \frac{+\ \textbf{T-A T-B T-C T-D (Euchlaena)}}{wx\ \ +\ \ +\ \ +\ \ +\ \ \textbf{(Zea)}}$$

Genes XY	Linkage phase	No. of plants				Recombinations		P value
		XY	*Xy*	*xY*	*xy*	No.	Per cent	
Wx T-A.......	R	90	64	64	55	145	53	.31
Wx T-B.......	R	77	77	61	58	135	50	.50
Wx T-C.......	R	87	67	64	55	142	52	>.50
Wx T-D.......	R	63	91	63	56	119	44	.05
T-A T-B......	C	73	81	65	54	146	54	.18
T-A T-C......	C	83	71	68	51	139	51	>.50
T-A T-D......	C	65	89	61	58	150	55	.10
T-B T-C......	C	70	68	81	54	149	55	.10
T-B T-D......	C	61	77	65	70	142	52	>.50
T-C T-D......	C	67	84	59	63	143	52	>.50

Table 30. Recombinations in the cross:

$$y\ pl\ \textbf{t-a t-b t-c t-d (Zea) x}\ \frac{+\ +\ \textbf{T-A T-B T-C T-D (Euchlaena)}}{Y\ Pl\ \ +\ \ +\ \ +\ \ +\ \ \textbf{(Zea)}}$$

Genes XY	Linkage phase	No. of plants				Recombinations		P value
		XY	*Xy*	*xY*	*xy*	No.	Per cent	
Y Pl..........	C	49	32	36	46	68	42	.01
Y T-A.........	R	57	24	50	32	89	55	.06
Y T-B.........	R	42	39	54	28	70	43	.03
Y T-C.........	R	54	27	42	40	94	58	.02
Y T-D.........	R	47	34	50	32	79	49	.50
Pl T-A.........	R	60	25	47	31	91	56	.08
Pl T-B.........	R	52	33	44	34	86	53	.25
Pl T-C.........	R	51	34	45	33	84	52	.50
Pl T-D.........	R	50	35	47	31	81	50	>.50
T-A T-B......	C	59	48	37	19	85	52	.38
T-A T-C......	C	57	50	39	17	89	55	.06
T-A T-D......	C	59	48	38	18	86	53	.25
T-B T-C......	C	45	51	51	16	102	63*	<.01
T-B T-D......	C	54	42	43	24	85	52	.38
T-C T-D......	C	52	44	45	22	89	55	.06

*Deviation in wrong direction for linkage.

Table 31. Recombinations in the cross:

$$su\ tu\ \textbf{t-a t-b t-c t-d (Zea) x}\ \frac{+\ +\ \textbf{T-A T-B T-C T-D (Euchlaena)}}{su\ Tu\ \ +\ \ +\ \ +\ \ +\ \ \textbf{(Zea)}}$$

Genes XY	Linkage phase	No. of plants					Recombinations		P value
		XY	*Xy*	*xY*	*xy*	Total	No.	Per cent	
Su Tu........	R	15	235	49	94	393	109	28	<.01
Su T-A.......	C	173	77	55	88	393	132	34	<.01
Su T-B.......	C	104	131	62	32	329*	193	59†	<.01
Su T-C.......	C	152	98	51	92	393	149	38	<.01
Su T-D.......	C	114	121	36	58	329*	157	48	.20
Tu T-A......	R	7	57	221	108	393	115	29	<.01
Tu T-C......	R	29	35	174	155	393	184	47	.22
T-A T-B.....	C	102	119	64	44	329*	183	56	.03
T-A T-C.....	C	109	119	94	71	393	213	54	.11
T-A T-D.....	C	83	138	67	41	329*	205	62†	<.01
T-B T-C.....	C	71	95	103	60	329*	198	60†	<.01
T-B T-D.....	C	68	98	82	81	329*	180	55	.07
T-C T-D.....	C	68	106	82	73	329*	188	57†	.01

**Tu* plants not included. †Deviation in wrong direction for linkage.

Table 32. Crossing-over between different translocation segments. Summary of four crosses

Segments *XY*	No. of plants					Recombinations		P value
	XY	*Xy*	*xY*	*xy*	Total	No.	Per cent	
T-A T-B.......	265	275	200	142	882	475	54	.11
T-A T-C.......	279	268	233	166	946	501	53	.07
T-A T-D.......	232	308	195	147	882	503	57*	<.01
T-B T-C.......	218	247	265	152	882	512	58*	<.01
T-B T-D.......	212	253	215	202	882	468	53	.07
T-C T-D.......	213	270	214	185	882	484	55*	<.01

*Deviation in wrong direction for linkage.

In the *B lg* cross there occurs a recombination percentage of 39 between *Lg* and T-B. This differs significantly from the 50 per cent expected from independent inheritance but it must be ruled out as a random fluctuation because T-B shows no linkage with gene *B* on the same chromosome. McClintock (1931b) has shown that the gene for liguleless lies very close to the end of chromosome 2, so that the translocation segment, in order to exhibit 39 per cent of crossing-over with liguleless, would probably have to reside between *Lg* and *B,* in which case it would show close linkage with gene *B*.

The next cross involving *wx* shows not a single recombination percentage differing significantly from the 50 per cent expected from independent inheritance. Apparently that part of the ninth teosinte chromosome which fails to pair with maize is not a translocation segment from Tripsacum but is merely a chromosome aberration of the kind sometimes found in pure corn, perhaps an inversion.

The cross of *Y Pl* and teosinte shows no indication of linkage with any of the four translocation segments.

When we come to the cross of *su Tu* with teosinte, we find four significant departures from independent inheritance. Sugary, *su*, is, of course, linked with *Tu;* T-A is linked with both *su* and *Tu;* T-C is linked with *su* and shows an additional indication of linkage with *Tu*. All of the data fit into the linkage map shown in Figure 77.

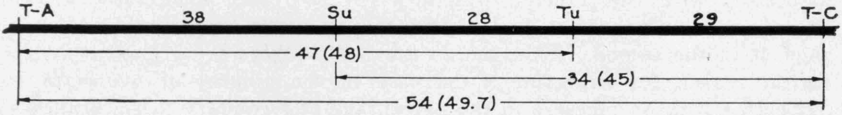

Fig. 77. Linkage map showing the relation of translocation segments A and C to the genes *Su* and *Tu* on chromosome 4. Values in parentheses are theoretical values obtained by combining intervening cross-over values.

It will be recalled that in the earlier studies on linkage of qualitative and quantitative characters in this same material, only the fourth chromosome showed strong indications of linkage. This fact is now accounted for. Two of the four translocation segments which differentiate Zea and Euchlaena are located at opposite ends of chromosome 4, so far apart that they show no linkage with each other but still close enough together to exhibit linkage with two genes near the middle of the chromosomes (Fig. 77).

It should be pointed out that an apparent linkage may be shown between two genes even when they are on different chromosomes, if they occur in excess of the theoretical expectation. This may account for some of the linkages found. It is equally true that if two genes are linked, any influence which causes an excess in one is also likely to cause an excess in the other, and the data from the teosinte-*su Tu* cross can be interpreted on this basis. Tests with other fourth-chromosome genes are needed, however, to establish completely the linkage between T-A, T-C, and the genes on the fourth chromosome.

The classification of the hybrid population into different groups on the basis of number and kind of translocation segments has been based largely on two characteristics, development of the glumes and number of rows of spikelets. Are any of the other differences between Zea and Euchlaena associated with these characters? Tables 33-36 and Figure 78 show that they are. When the same data which we had previously used in studying linkage between qualitative and quantitative factors are averaged for the five different groups of plants having none, one, two, three, and four translocation segments, respectively, we find an almost perfect correlation in some cases between the number of segments and the expression of the characteristics which differentiate the two genera.

In the case of some of the ear characters, such as length, for example, it might be suggested that the longer ears were assigned to the first classes and the shorter ears to the last classes, and thus a correlation would obviously be shown. This is true. But the ears were not classified primarily for length, and some of the ears in class three, for example, are longer than some of those in class two (see Fig. 76). And when it is considered further that the final classification differs significantly from a normal frequency distribution, it does not seem possible that five classes could have been arbitrarily arranged so accurately that the averages of the different groups would fall into so nearly a straight line.

It may also be suggested that the number of ears is physiologically associated with the number of ovules per ear, and since these groups show a regular gradation in the first characteristic they would naturally show it in the second. This, too, is true. But there is no known physiological reason for expecting a decrease in the number of ovules to be associated with an increase in the percentage of secondary tassel branches. Yet this is exactly what has occurred.

It seems obvious that in classifying the plants of this population on the basis of the few so-called essential differences between Zea and Euchlaena, they also have been classified on the basis of all other characteristics upon which measurements were available. In other words, the same genes, or same groups of genes, which are responsible for the differences between prominent horny glumes and inconspicuous membranaceous glumes are also responsible for days to anthesis, number of

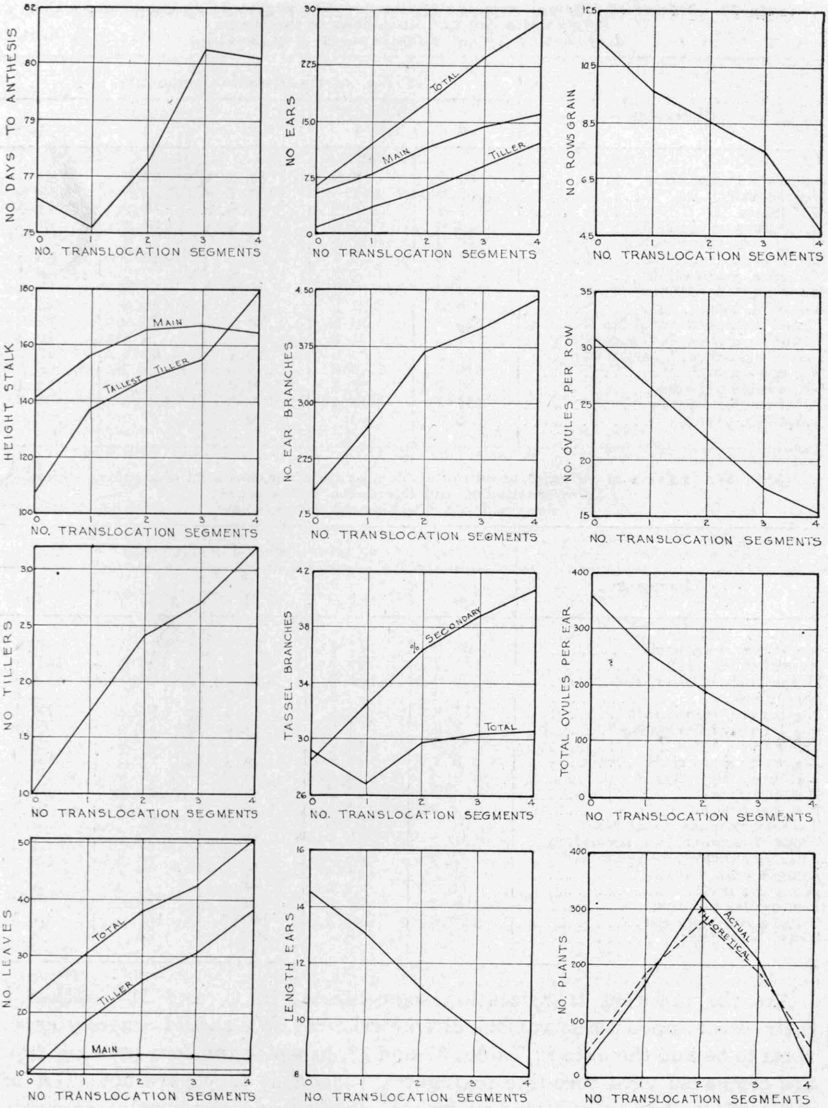

Fig. 78. **The effect of number of translocation segments from teosinte upon various characteristics which distinguish the two genera, Zea and Euchlaena.**

tillers, percentage of secondary tassel branches, and all the other characteristics which had previously been considered, but which had been completely ignored in arriving at the new classification.

Table 33. Effects of different numbers of translocation segments on characters which differentiate Zea and Euchlaena in the cross:
***b lg* (Zea) x [*b Lg* (Euchlaena) x *B lg* (Zea)]**

Character	No. of translocation segments				
	0	1	2	3	4
No. days to anthesis	81.7	78.9	81.9	83.9	82.3
Height stalk, cm	152.0	144.5	152.7	153.5	151.6
No. tillers	1.7	3.2	4.6	4.9	4.7
No. leaves, main stalk	12.0	10.6	11.0	10.8	10.7
No. leaves, tiller stalks	16.0	32.5	46.5	51.4	51.9
No. leaves, total	28.0	43.1	57.5	62.2	62.6
No. ears, main stalk	4.3	4.7	6.6	7.7	9.4
No. ears, tiller stalks	1.7	6.5	10.1	13.8	13.3
No. ears, total	6.0	11.2	16.7	21.5	22.7
Tassel branches, total No.	23.3	20.3	24.1	25.9	27.6
Tassel branches, No. secondary	4.3	4.8	7.4	8.4	10.3
Tassel branches, % secondary	18.5	23.6	30.7	32.4	37.3
No. rows grain	10.7	9.8	8.5	7.7	5.4
No. ovules per row	35.7	27.8	20.4	15.1	13.3
Total ovules per ear	381.3	269.4	172.8	114.8	69.7
Total No. plants	3	30	50	27	7

Table 34. Effects of different numbers of translocation segments on characters which differentiate Zea and Euchlaena in the cross:
***wx* (Zea) x [*Wx* (Euchlaena) x *wx* (Zea)]**

Character	No. of translocation segments				
	0	1	2	3	4
No. days to anthesis	69.2	71.4	72.8	75.5	76.8
Height stalk, cm	131.7	145.5	154.9	158.0	161.5
Height tallest tiller, cm	109.0	131.9	136.0	154.3	185.0
No. tillers	.2	.8	1.0	1.5	2.7
No. leaves, main stalk	11.9	12.1	12.3	12.2	12.2
No. leaves, tiller stalks	2.4	7.6	11.2	16.6	30.2
No. leaves, total	14.3	19.7	23.5	28.8	42.4
No. ears, main stalk	8.1	13.8	19.1	25.3	28.0
No. ears, tiller stalks	.4	2.6	4.2	9.6	21.0
No. ears, total	8.5	16.4	23.3	34.9	49.0
No. ear branches	2.8	3.6	4.8	5.1	6.5
Tassel branches, total No.	33.0	30.0	33.0	32.2	29.3
Tassel branches, No. secondary	10.5	10.7	12.3	13.5	11.5
Tassel branches, % secondary	31.8	35.7	37.3	41.9	39.2
Length ears, cm	13.2	11.4	10.5	9.7	8.4
No. rows grain	11.5	9.5	8.5	7.0	4.3
No. ovules per row	26.1	23.8	21.2	18.8	15.2
Total ovules per ear	305.0	223.9	180.4	132.5	64.3
Total No. plants	12	58	104	93	6

Are the different translocation segments A, B, C, and D identical in their effects upon these various characteristics? We should scarcely expect them to be and the data in Tables 37 and 38, in which the four primary types are compared with corn-like segregates, show that they yare not. T-A has more effect than any others on height of tiller and per cent of secondary tassel branches. T-B has more effect than others on the tillering habits, size of ear, and number of ovules. T-C has its greatest effects on days to anthesis and length of ear, being the only one that causes an increase in the length of the ear. T-D has the least effect of any of the segments on many characters but apparently has more effect on number of tassel branches than do any of the others.

Table 35. Effects of different numbers of translocation segments on characters which differentiate Zea and Euchlaena in the cross:
su tu (**Zea**) **x** [*Su tu* (**Euchlaena**) **x** *su Tu* (**Zea**)]

Character	No. of translocation segments				
	0	1	2	3	4
No. days to anthesis	77.7	76.0	77.8	82.0	81.5
Height stalk, cm	150.5	166.2	176.8	175.3	168.0
Height tallest tiller, cm	106.0	142.7	160.4	155.7	173.2
No. tillers	1.0	1.2	1.5	1.7	2.3
No. leaves, main stalk	13.0	13.4	13.8	13.8	13.0
No. leaves, tiller stalks	11.3	14.4	19.3	23.2	32.2
No. leaves, total	24.3	27.8	33.1	37.0	45.2
No. ears, main stalk	4.2	6.4	9.5	10.4	11.3
No. ears, tiller stalks	.7	2.1	3.7	4.3	2.7
No. ears, total	4.9	8.5	13.2	14.7	14.0
No. ear branches	.8	1.7	2.5	2.9	2.2
Tassel branches, total No	31.2	30.2	32.3	33.1	34.7
Tassel branches, No. secondary	10.2	10.5	12.6	13.4	15.5
Tassel branches, % secondary	32.7	34.8	39.0	40.5	44.7
Length ears, cm	15.8	14.8	11.9	9.6	8.2
No. rows grain	12.3	9.8	8.8	7.8	4.3
No. ovules per row	30.5	28.0	24.5	18.8	17.3
Total ovules per ear	386.0	275.9	214.9	147.2	78.0
Total No. plants	6	77	172	91	6

Table 36. Effects of different numbers of translocation segments on the characters which differentiate Zea and Euchlaena, summary of three crosses

Character	No. of translocation segments				
	0	1	2	3	4
No. days to anthesis	76.2	75.4	77.5	80.5	80.2
Height stalk, cm.*	141.1	155.9	165.9	166.7	161.8
Height tallest tiller, cm.*	107.5	137.3	148.2	155.0	179.1
No. tillers	1.0	1.7	2.4	2.7	3.2
No. leaves, main stalk	12.3	12.0	12.4	12.3	12.0
No. leaves, tiller stalks	9.9	18.2	25.7	30.4	38.1
No. leaves, total	22.2	30.2	38.1	42.7	50.1
No. ears, main stalk	5.5	8.3	11.7	14.5	16.2
No. ears, tiller stalks	.9	3.7	6.0	9.2	12.3
No. ears, total	6.5	12.0	17.7	23.7	28.6
No. ear branches*	1.8	2.7	3.7	4.0	4.4
Tassel branches, total	29.2	26.8	29.8	30.4	30.5
Tassel branches, No. secondary	8.3	8.7	10.8	11.8	12.4
Tassel branches, % secondary	28.4	32.5	36.2	38.8	40.7
Length ears, cm.*	14.5	13.1	11.2	9.7	8.3
No. rows grain	11.5	9.7	8.6	7.5	4.7
No. ovules per row	30.8	26.5	22.0	17.6	15.3
Total ovules per ear	357.4	256.4	189.7	131.5	70.7
Total No. plants	21	165	326	211	19

*No data from *B lg* cross for this character.

If these effects could be averaged it would probably be shown that T-B has the greatest effect, T-C next, T-A slightly less, and T-D the least. In any case, there are appreciable differences between the different segments in their effects, a fact indicating that they may differ in number and kind of genes which they bear, though they are all alike in bearing genes which affect the characteristics differentiating Zea and Euchlaena.

Table 37. Comparison, in characters which differentiate Zea and Euchlaena, of plants with one translocation segment and those with none

Character	Translocation segment present				
	None	T-A	T-B	T-C	T-D
No. days to anthesis	73.4	73.8	75.2	75.8	74.5
Height stalk, cm	140.0	157.2	142.3	160.3	155.8
Height tallest tiller, cm.*	107.0	148.9	120.2	140.3	137.2
No. tillers	.7	1.3	1.5	1.4	1.4
No. leaves, main stalk	12.2	12.4	11.7	12.8	12.3
No. leaves, tiller stalks	6.9	14.6	16.3	15.5	14.9
No. leaves, total	19.1	27.0	28.0	28.3	27.2
No. ears, main stalk	6.4	9.7	9.5	7.6	8.4
No. ears, tiller stalks	.7	3.3	4.0	2.4	3.1
No. ears, total	6.6	13.0	13.5	10.0	11.5
No. ear branches*	2.1	2.9	2.9	2.2	2.3
Tassel branches, total No	31.1	28.9	27.1	29.5	26.4
Tassel branches, No. secondary	9.5	10.2	8.4	9.9	7.0
Tassel branches, % secondary	28.8	33.0	29.2	32.4	32.0
Length ears, cm.*	14.0	13.4	9.8	15.1	13.3
No. rows grain	11.6	9.6	9.8	9.8	9.4
No. ovules per row	28.7	28.3	19.9	28.2	28.4
Total ovules per ear	339.0	274.4	193.8	276.2	264.1
Total No. plants	21	45	35	60	25

*No data from *B lg* cross for this character.

Table 38. Effects of different translocation segments on characters which differentiate Zea and Euchlaena, in terms of percentage differences between plants with one segment and those with none

Character	Percentage difference			
	T-A	T-B	T-C	T-D
No. days to anthesis	.5	2.5	3.3	1.5
Height stalk	12.3	1.6	14.5	11.3
Height tallest tiller*	39.2	12.3	31.1	28.2
No. tillers	198.5	229.9	204.5	209.0
No. leaves, main stalk	1.6	4.1	4.9	.8
No. leaves, tiller stalks	111.6	136.2	124.6	115.9
No. leaves, total	41.4	46.6	48.2	42.4
No. ears, main stalk	51.6	48.4	18.8	31.3
No. ears, tiller stalks	371.4	471.4	242.9	342.9
No. ears, total	97.0	104.6	51.5	74.2
No. ear branches*	38.1	38.1	4.8	9.5
Tassel branches, total No	— 7.1	—12.9	— 5.1	—15.1
Tassel branches, No. secondary	7.4	—11.6	4.2	— 5.3
Tassel branches, % secondary	14.6	1.4	11.3	11.1
Length ears*	— 4.3	—30.0	7.9	— 5.0
No. rows grain	—17.2	—15.5	—15.5	—19.0
No. ovules per row	— 1.4	—30.7	— 1.7	— 1.1
Total ovules per ear	—19.1	—42.8	—18.5	—22.1
Total No. plants	45	35	60	25

*No data from *B lg* cross for this character.

It should be pointed out that throughout these studies we have been measuring only those characteristics in which Euchlaena is partially or completely dominant. This probably accounts for the fact that there is so little difference between the two extremes in number of days to anthesis. The late maturity of Euchlaena, which is in reality a strong response to short days, is recessive to the weak response of Zea (cf. Langham 1938). Hence the only segregation expected when the F_1 hybrid is backcrossed with maize is the segregation of genes involved in time of maturity exclusive of those governing the reaction to short days. In spite of this fact the four translocation segments do, in some characteristics, account for almost all of the differences which exist between pure corn and the F_1 hybrid of corn and teosinte. Although there are undoubtedly numerous other genes or short chromatin segments by which the two genera differ, these four segments account for most of the differences which distinguish Euchlaena from Zea, for in no other way is it possible to account for the frequent recovery of the parental types.

THE ORIGIN OF TEOSINTE

The Intermediate Nature of Euchlaena Mexicana

Once we consider seriously the hypothesis that Euchlaena is nothing more than a hybrid of Zea and Tripsacum, we discover an amazing amount of evidence in its support. The hybrid of Zea x Tripsacum crosses as readily or perhaps more readily with Euchlaena than with either of its parents, a fact which may suggest that Euchlaena, like the hybrid, is a mixture of Zea and Tripsacum genes.

Segregates from the hybrid Zea x Euchlaena are, in some cases, duplicated by segregates from the hybrid Zea x Tripsacum (Figs. 84-85). This shows that Euchlaena and Tripsacum possess genes with identical effects.

In the trigeneric hybrid resulting from this pollination, the chromosomes of Euchlaena, though bearing genes for characters identical with those of Tripsacum, pair completely with the Zea chromosomes. This suggests that Euchlaena may be essentially Zea with a few Tripsacum genes. The fact that a few Tripsacum chromosomes have a relatively greater effect than a large number when superimposed on maize, or that one or two Tripsacum chromosomes may have a greater effect than all of them, on characteristics which distinguish the two genera, suggests that a transfer of a small amount of Tripsacum chromatin to Zea might easily bring about the conversion of Zea to Euchlaena. Finally, the fact that Euchlaena differs from Zea primarily by four segments of chromatin all bearing Tripsacum genes or genes with Tripsacum effects, almost clinches the argument.

But there are other isolated bits of evidence which support the hypothesis. Why does Euchlaena occupy such a restricted range? It occurs wild (or at least thoroughly established as an escape) only in a limited area in western Guatemala, and its appearance in other regions is sporadic. Yet it would probably be capable of maintaining itself in the wild in many parts of North and South America. Weatherwax (1935) reports that Florida teosinte is persisting as an escape near Lake Apopka in Florida, and Kempton and Popenoe (1937) mention that perennial teosinte has become established in James Island off the coast of South Carolina. We can cite similar instances in Texas, for at College

Station, Florida teosinte has volunteered and maintained itself for at least one season in competition with other grasses, and at Texas Substation No. 3 at Angleton, Texas, a colony of perennial teosinte has survived and spread during a period of seven years. Why should a genus with these apparent capabilities of survival be so restricted in its range? Weatherwax (1935) suggests that Euchlaena has retreated before the onslaughts of the large grazing animals introduced into America by the Europeans. Another interpretation, and perhaps a more plausible one, is that Euchlaena is a young genus which has appeared on the scene too recently to have had an opportunity to spread. It cannot be denied that many American plants have tended to disappear since European animals were introduced; Tripsacum, for example, once abundant in the Blacklands of Texas, is now almost absent there. Yet these disappearing species are still found in protected sites, such as railroad rights-of-way, and are recorded by early botanical explorations.

Perhaps the most convincing evidence in favor of the hypothesis of a hybrid origin of Euchlaena is the fact that it is intermediate between Zea and Tripsacum in so many characteristics. In a previous paper (Mangelsdorf and Reeves 1935) we had pointed out, without realizing its significance, that Euchlaena resembles either Zea or Tripsacum in all the characteristics which were studied except the presence of secondary branches in the tassel. When we attempt to list all of the characteristics in which Euchlaena is intermediate between the two putative parents, or in which it resembles one or the other of the two parents, we discover that Euchlaena has very few, if any, distinctive characteristics of its own. Thirty-four characteristics in which Zea and Tripsacum differ are listed in Table 39.

In most cases where an intermediate condition is possible, Euchlaena is intermediate. In other characteristics it is like one or the other of the two putative parents. Even in the latter characteristics, however, it frequently shows a tendency to be intermediate. Zea, for example, is an annual, Tripsacum a perennial; Euchlaena is an annual but a long-lived one. It has, in fact, been described by earlier botanists as both annual and perennial (cf. Kempton and Popenoe 1937). Euchlaena resembles Zea in possessing a terminal inflorescence comprised exclusively of staminate spikelets, but the inflorescence itself is like that of Tripsacum in lacking a conspicuous central spike and in having a short branching space. It resembles Tripsacum in having a small number of ovules on each spike and in having the seeds enclosed in horny glumes, but resembles Zea in having the spikes enclosed in shucks, which characteristic is itself an anomaly, for shucks are certainly not necessary to seeds already protected by a stony shell, and they interfere to some extent with the mechanism for dispersal provided by the brittle rachis. Small wonder that some competent taxonomists have regarded Euchlaena as a "queer" genus.

Table 39. Comparison of some of the distinguishing characteristics of Zea, Euchlaena, and Tripsacum

Characteristic	Zea	Euchlaena	Tripsacum
Growth habit	annual	long-lived annual	perennial
Root stocks	absent	absent	present
No. tillers	few	intermediate	many
Height tillers in relation to main stalk	short	tall	tall
Width leaves in relation to length	wide	intermediate	narrow
No. nerves per unit of width	few	intermediate	many
Central spike in tassel	present	absent or small	absent
Branching space on tassel	long	intermediate	short
No. of tassel branches	intermediate	many	few*
No. secondary tassel branches	few	many	none*
Pistillate spikelets in tassel	absent	absent	present
Pedicels on second staminate spikelet	long	intermediate	short
Size of pollen	large	intermediate	small
Meiosis in relation to emergence of inflorescence	early	intermediate	late
Silks or anthers appear first	anthers	silks	silks
Lateral inflorescence enclosed in husks	enclosed	enclosed	naked
No. chromosome knobs	few	intermediate	many
Position of majority of knobs	internal	internal & terminal	terminal
Secondary branching, lateral inflorescence	latent	common	rare
Length of internodes, lateral branches	short	intermediate	long
Length of styles	long	intermediate	short
Hairs on styles	few	intermediate	many
Styles fused or separate	fused	fused	separate
Staminate spikelets on lateral inflorescence	none	few	many
Pistillate spikelets paired or single	paired	single	single
No. rows pistillate spikelets	many	two	two
Glumes horny or membranaceous	membranaceous	horny	horny
Seeds naked or enclosed	naked	enclosed	enclosed
Rachis solid or brittle	solid	brittle	brittle
Resistance to drought and heat	susceptible	intermediate	resistant
Resistance to frost	susceptible	intermediate	resistant
Resistance to *Puccinia polysora*	resistant	resistant	susceptible
Resistance to *Puccinia sorghi*	susceptible	susceptible	resistant
Resistance to *Perigrinis maidis*	susceptible	intermediate	resistant

*This is true of *T. dactyloides*. Does not apply to *T. laxum* or *T. pilosum*.

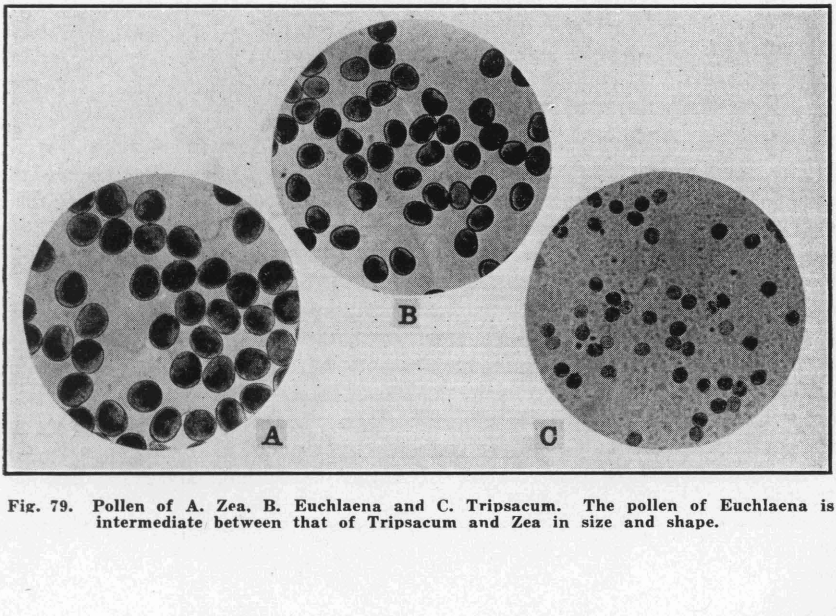

Fig. 79. Pollen of A. Zea, B. Euchlaena and C. Tripsacum. The pollen of Euchlaena is intermediate between that of Tripsacum and Zea in size and shape.

Euchlaena resembles Zea in concentrating the pistillate spikelets on the lateral inflorescences, but even here the influence of Tripsacum is evident, for almost all lateral inflorescences of Euchlaena bear a few functional or aborted staminate flowers. Euchlaena resembles Zea in the complete fusion of the two parts of the bipartite style, but is like Tripsacum in possessing relatively short, thick styles profusely covered with hairs. Even the pollen of Euchlaena is intermediate in size and shape between that of Zea and Tripsacum (Fig. 79), although it shows a much closer resemblance to Zea than to Tripsacum.

The susceptibility of the two genera to various diseases is of some interest. Seymour (1929) lists the following diseases as occurring on Euchlaena and Tripsacum.

Fungi on *Euchlaena mexicana*
- **Helminthosporium turcicum* Pass
- **Ophiobolus heterostrophus* Drechsler
- **Physoderma Zeae-maydis* Shaw
- **Puccinia Sorghi* S.
- *Septoriella mexicana* Sacc.
- **Sclerospora graminicola* (Sacc.) Schrt.
- **Poria corcos* Wolf
- **Ustilago Zeae* (Beckm.) Ung.
- *Ustilago Kellermanii* G. P. Clinton
- *Ustilago Euchlaenae* Arcang.

Fungi on Tripsacum spp.
- *Claviceps purpurea* (Fr.) Tul.
- **Colletotrichum graminicola* (Ces.) G. W. Wilson
- *Claviceps Tripsaci* Stevens and Hall
- **Epicoccum neglectum* Desm.
- **Puccinia pallescens* Arth.
- *Puccinia Tripsaci* Diet. and Holw.
- *Puccinia polysora* Underw.
- *Ustilago dieteliana* Henn.

The species of fungi found on these two genera and also known to occur on Zea are distinguished by an asterisk. Of the ten species occurring on Euchlaena, seven are also known to occur on Zea. Of the eight occurring on Tripsacum, three also occur on Zea, but none are known to occur on Euchlaena. At least two of these three, however, Colletotrichum and Epicoccum, are widely distributed on many genera of host plants, and undoubtedly occur in Euchlaena, but have simply never been reported.

Two of the rusts, *Puccinia sorghi* and *Puccinia polysora*, are quite definite in their host relationships. *Puccinia sorghi* is frequently found on Zea, Euchlaena, and *Sorghum vulgare*, but never on Tripsacum; *Puccinia polysora* is found on various species of Tripsacum and on *Erianthus divaricatus*, a relative of sugar cane, but never on Zea or Euchlaena.

Briefly summarized, the facts indicate that Zea and Euchlaena are quite similar in susceptibility to various diseases, while Tripsacum is in a somewhat different category. We suspect, however, that additional studies will show greater similarities than are now known to exist, and it is not improbable that one of the three smuts reported to occur on Euchlaena will be found to be identical with the smut of Tripsacum.

Resistance of the three genera to frost is an especially interesting characteristic because it is one in which we had predicted that Euchlaena would be found to be intermediate. We had previously considered Euchlaena as a tropical or semi-tropical plant with no marked resistance to frost; but when its intermediate nature in other characteristics became evident, we suspected that it would prove to be more resistant to frost than Zea and less resistant than Tripsacum. We were very fortunate in November of 1937 in having a frost with a differential killing effect; it injured maize plants severely, several species of Tripsacum only slightly, and affected Euchlaena in an intermediate fashion, injuring it less severely than maize but more severely than Tripsacum.

Many additional characteristics in which Euchlaena is intermediate between Zea and Tripsacum could be mentioned—shape of glumes (Fig. 80), structure of the leaves, hairs on the leaves and silks (Fig. 81)—but only one more will be discussed, its attractiveness to certain insects, especially the corn leaf hopper *Peregrinus maidis*. This insect is a serious pest to corn grown in the greenhouse, and sometimes also attacks Tripsacum; but seldom if corn plants are available at the same time, for they are greatly preferred. When all three genera are growing together in the presence of an infestation of leaf hoppers, corn is covered with insects, Euchlaena has a moderate number, and Tripsacum has few or none.* It is of interest to note in this connection that Venkatraman and Thomas (1932) observed an infestation of *Aphis maidis* on sorghum while sugar cane and sugar cane-sorghum hybrids were free. They cited this as an illustration of an insect's ability to discover more quickly than a morphological botanist the real nature of a population.

Weatherwax (1918) contends that the fact that a species is intermediate between two others is not good evidence that it is a hybrid between them. This certainly is true if only one or several characteristics are considered. On the other hand if Zea, Euchlaena, and Tripsacum had descended along divergent lines from a remote common ancestor, as Weatherwax (1918, 1935) has assumed, it is inconceivable, and in fact mathematically almost impossible, that Euchlaena should not have acquired some distinctive characteristics of its own, which were common to neither Zea nor Tripsacum. Yet it apparently has no such characteristics. It is true that Euchlaena differs from both Zea and *T. dactyloides* in having a profusely branched tassel with a large percentage of secondary branches in the tassel, but even here it does not differ from *T. pilosum*, which is common in Central America. Also Euchlaena has smaller rachis

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*Gernert (1912) has reported that teosinte is also more resistant to Aphis than maize.

Fig. 80. Staminate spikelets of Andean maize, North American maize, teosinte and Tripsacum. Teosinte is intermediate between maize and Tripsacum in shape of glumes and pubescence on glumes. North American maize in turn is intermediate between teosinte and Andean maize in these characteristics. (See p. 252.)

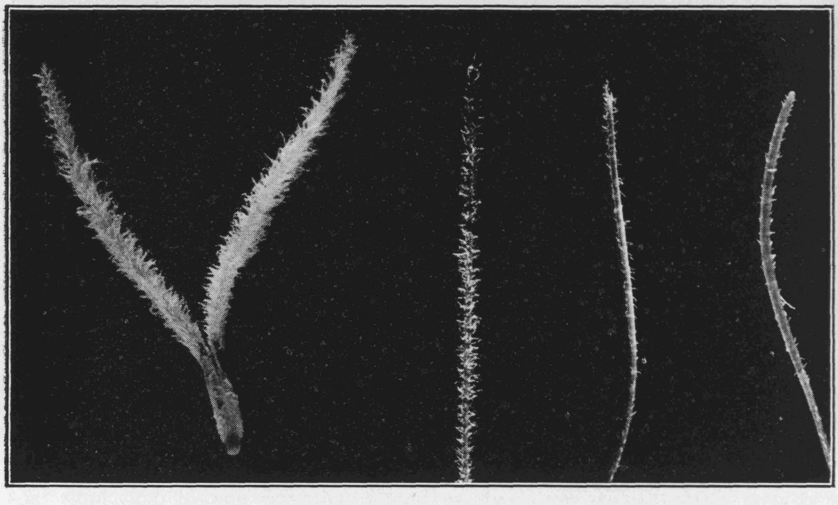

Fig. 81. Styles of Tripsacum, teosinte, North American maize, and Andean maize. Note that teosinte is definitely intermediate between Tripsacum and maize in the profusion of stylar hairs. North American maize is intermediate between teosinte and Andean maize in this characteristic.

segments than those of most species of Tripsacum and the segments are triangular instead of trapezoidal as are those of Tripsacum; but these differences may be meaningless, for we have no way of anticipating exactly what type of structure is to be expected when the genes for prominent horny glumes and brittle rachis are superimposed upon the genetic complex of Zea. Furthermore, there are types of corn in which the segments of the culm, the internodes, approach the triangular shape (cf. Kempton 1921a, Plate IV); so that it is not particularly surprising to find triangular rachis segments in Euchlaena.

Another characteristic in which Euchlaena appears at first glance to differ from Zea and Tripsacum, but in which, upon closer examination, it proves to be intermediate, is in the secondary and tertiary branching of the lateral inflorescences (Figs. 82-83). Tripsacum and Zea seldom show secondary branching, while Euchlaena under normal conditions branches profusely. Zea, however, possesses latent branches at every node, and when the terminal inflorescence of the lateral branch is injured, or is not pollinated, or bears only a few seeds, the latent branches immediately appear. The condition in Euchlaena is exactly the one which we should expect from combining the small spike of Tripsacum with the branching potentialities of Zea. Furthermore the length of the internodes on the lateral branches of Euchlaena are intermediate between those of Zea and Tripsacum. All characteristics considered, the lateral branches of Euchlaena, though quite different from those of either Zea or Tripsacum, approach an intermediate condition as closely as such a condition can be approached by combining two widely different structures.

Although Euchlaena shows an intermediate condition between Zea and Tripsacum in most characteristics, there are four in which it is almost identical with Tripsacum—prominent horny glumes, brittle rachis, distichous arrangement, and the unpaired condition of the spikelets. These are, it will be recalled, the same four characteristics which we have previously listed as constituting the essential differences between Zea and Euchlaena. It appears that the only plants from the natural hybrid of Zea and Tripsacum which were capable of surviving in nature were those which had received these four Tripsacum characteristics. That Euchlaena shows other characteristics of Tripsacum as well, implies that these four characteristics were transferred to Zea, not as single genes, but as sections of chromatin bearing other genes in addition to those governing the four essential characteristics. Thus Euchlaena is identical with Tripsacum in these four characteristics but much more like Zea than Tripsacum in almost all others. In other words, Euchlaena appears to be nothing more than Zea with a slight infection of Tripsacum germplasm.

The Method of Origin

The results already presented indicate in a general way the method of origin of Euchlaena. It is assumed that the natural hybridization of Tripsacum and Zea occurred somewhere in Central America when plants of the two genera were brought in contact with each other in great numbers. Natural hybridization does not occur in North America because the two genera bloom at different periods, the common species of Tripsa-

Fig. 82. The branching habit of teosinte. A lateral branch occurs at every node of the stalk; secondary branches usually occur at every node of the branch.

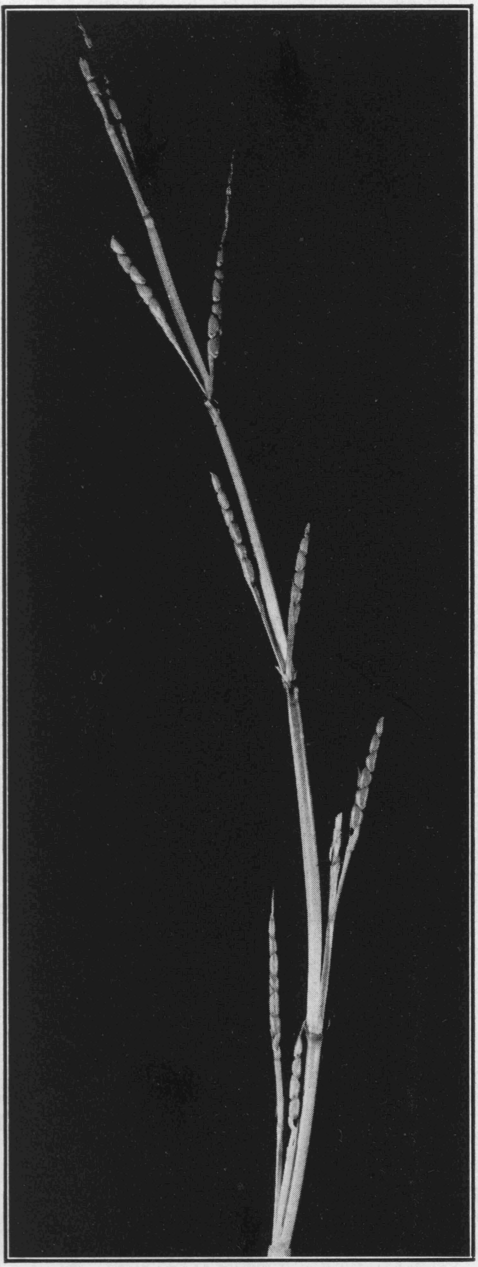

Fig. 83. Lateral inflorescence of Florida teosinte with leaf sheaths removed. One or more secondary branches usually occur at each node.

cum, *T. dactyloides*, usually having completed its blooming period before that of Zea has begun. The Central American species of Tripsacum are quite late in flowering, at least when grown in the United States; and since many of the Central American maize varieties are also quite late (Kuleshov 1933), and as several successive plantings of the earlier varieties are frequently made (Morley 1920), the blooming period of Zea and Tripsacum frequently coincide.

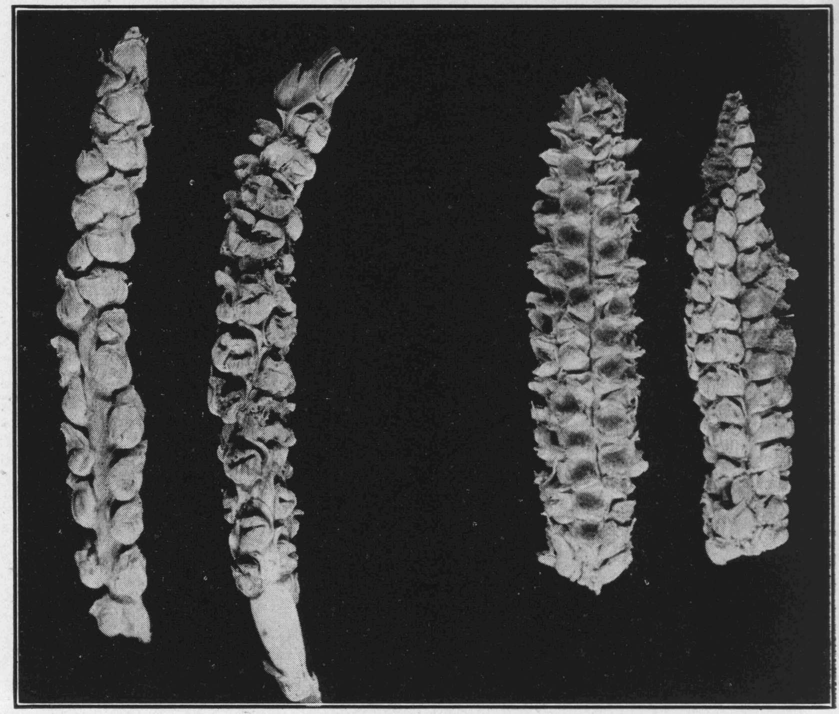

Fig. 84. Many of the segregates from the Zea-Tripsacum cross can be almost duplicated by segregates from Zea-Euchlaena crosses, indicating that Euchlaena and Tripsacum possess genes with similar or identical effects. Two matched pairs of segregates are illustrated above. In both cases the Zea-Tripsacum segregates are shown at left.

When the suggestion that Euchlaena might have originated as a cross of Zea and Tripsacum was first made to us by Dr. Edgar Anderson, we dismissed it as untenable on the grounds that any hybrid so difficult to produce could never have occurred in nature, a conclusion which Weatherwax (1935) has also reached.

Further consideration of the problem, however, leads to the conclusion that natural hybridization is not out of the question. As in the case of wheat and rye (cf. Backhouse 1916) there is a great difference in the

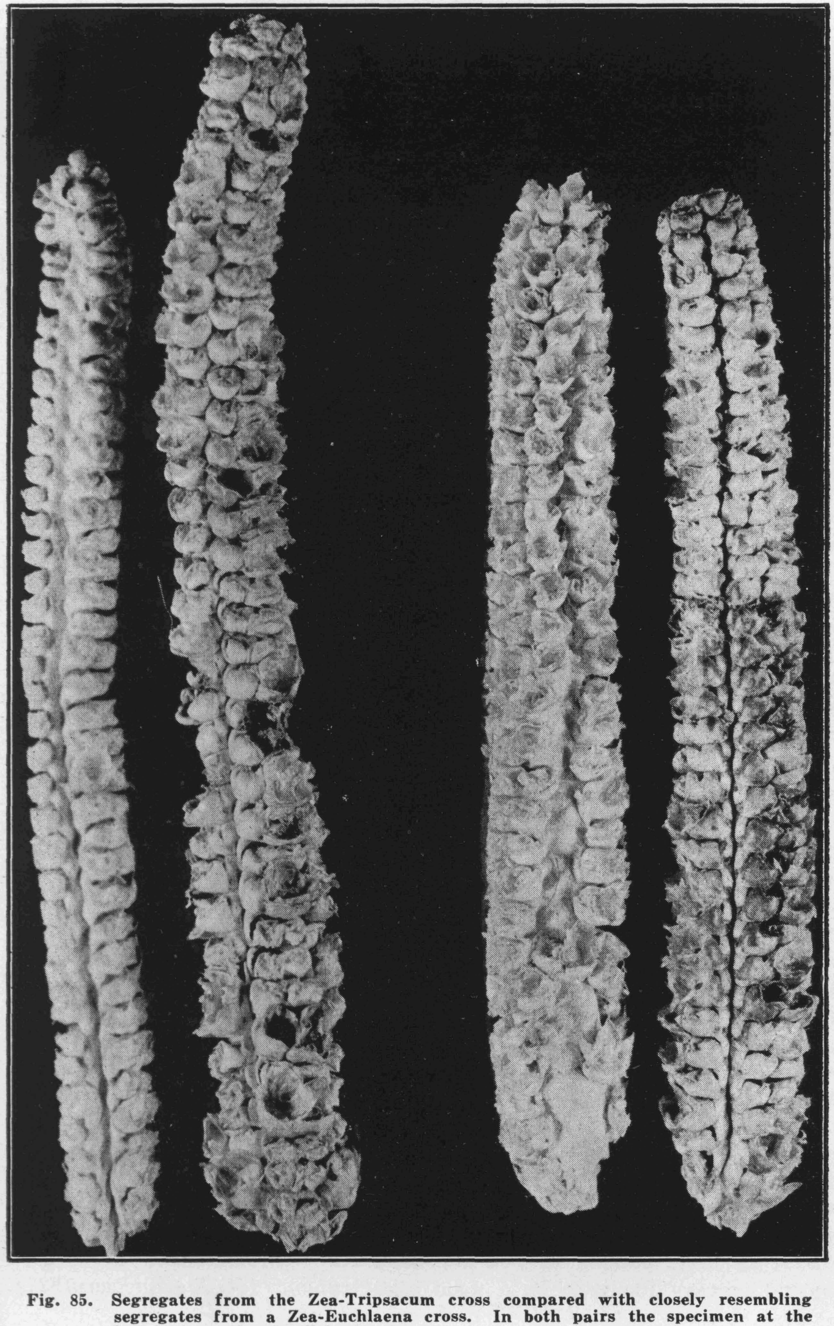

Fig. 85. Segregates from the Zea-Tripsacum cross compared with closely resembling segregates from a Zea-Euchlaena cross. In both pairs the specimen at the left is from the Zea-Tripsacum cross.

"crossability" of corn varieties, as indicated by our previous studies (1931); and there are undoubtedly some which will hybridize with Tripsacum more easily than those which we have included in our tests. If the length of the styles remains an important consideration, we must consider the small-eared varieties from the Andean region with their correspondingly short husks, varieties in which the distance from the exposed silks to the uppermost ovaries on the ear is but little, if any, greater than the distance which the Tripsacum pollen tube must traverse in fertilizing its own ovules. Furthermore, as we shall show later, the complete sheathing of the ears by the husks is probably a comparatively recent development which has come about since corn has been domesticated. Even today many ears are encountered in which the shucks are too short to cover the uppermost ovaries and it is quite likely that these types were more frequent at an earlier period than they are now. Finally, we can assume, if necessary, that grasshoppers or other leaf-eating insects destroyed the shucks and shortened the styles very much as we have done in our experiments. It is not unusual in the South for the larvae of the corn ear worm *Heliothis obsoleta* F. to pentrate the shucks, leaving a hole from which receptive silks sometimes emerge. Plagues of locusts are not uncommon in Central America and at least one student of Maya history (cf. Anon. 1938) suggests that it may have been locust plagues which led to the abandonment of the cities of the Old Maya Empire.

Perhaps a more serious difficulty is the fact that all of the Central American forms of Tripsacum which we have studied are tetraploid and the hybrid of Zea with the tetraploid *T. dactyloides* is completely sterile. We have, however, no assurance that all Central American forms of Tripsacum are tetraploid or that all hybrids of Zea with tetraploid forms of Tripsacum are sterile. Both of these are subjects for additional investigation.

One possible method by which Euchlaena may have originated has already been suggested—the repeated backcrossing of the partially fertile F_1 hybrid of diploid Zea x diploid Tripsacum with its Zea parent. Another method which occurs to us is a hybridization of tetraploid maize and tetraploid Tripsacum. The latter is common in Central America, and the former, though it has never been discovered in nature, is readily produced by heat treatment (Randolph 1932), a circumstance which suggests that it might occasionally arise spontaneously. Tetraploid maize and tetraploid Tripsacum hybridize rather readily, if we may judge from a single season's attempts with a rather limited population. Though we have not succeeded in bringing plants of this cross to maturity, we had no difficulty in obtaining hybrid seeds, and failure to secure living hybrid plants was due to fungus infection in the seedlings rather than to the inherent weakness of the hybrid. We anticipate that this tetraploid hybrid when finally obtained will be almost completely fertile and true-breeding, for if our cytological studies on the diploid hybrid are a criterion, we shall find very little pairing of Zea and Tripsacum chromosomes, and such a hybrid is very likely to be a good allotetraploid (cf. Darlington 1937).

If this allotetraploid is crossed with maize, there will, however, if again our previous cytological studies are a criterion, be some association and exchange of chromatin between the Zea and Tripsacum chromosomes, so that the repeated backcrossing of this hybrid with maize should result in types of maize in which the maize germplasm has become contaminated with small segments of Tripsacum chromatin. If these segments bear genes which bring about the expression of characters which provide protection for the seed and a means of dispersal, we should have a Euchlaena-like plant produced.

A tetraploid fertile hybrid of Zea and Tripsacum should be capable of persisting almost indefinitely in nature, and if Euchlaena originated from such a hybrid it is not inconceivable that the hybrid still exists. It is most likely to be found, we suspect, comprising a small colony in the region near San Antonio Huixta, where Kempton and Popenoe (1937) found Euchlaena the dominant species.

There are several types of Euchlaena in existence. The Mexican teosintes differ quite markedly from the Guatemalan forms, both in gross morphology and chromosome morphology. This might suggest that the cross of Zea and Tripsacum occurred repeatedly and that in each case the final survivors, though differing in many genes, were alike in receiving certain essential characteristics from Tripsacum. Another interpretation, and a far more plausible one, we believe, is that the hybrid occurred only once, but that in subsequent repeated hybridizations of maize and the new genus Euchlaena, the chromatin segments from Tripsacum have become superimposed upon a number of different types of corn. Associated with the repeated backcrossing of Euchlaena with maize has probably also been a reduction in the size of the translocation segments. We have cited several instances in which segments have lost part of their characteristic effects, presumably by the loss of part of the genes. A single cross of Durango teosinte and maize which we have studied shows that the distinctions among the four primary classes each involving one translocation segment are much less clear-cut than are those in the cross of Florida teosinte with maize. This loss of part of the segments would be a natural consequence of repeated hybridization with maize and the segments might become shortened almost indefinitely so long as the genes for horny glumes and brittle rachis remained. Thus we may assume that the Chalco teosinte, one of the most maize-like forms so far discovered, differs from the teosinte of San Antonio Huixta not only in the type of maize upon which the Tripsacum segments have been superimposed, but also in the actual amount of Tripsacum chromatin which has been added to or substituted for the maize germplasm. This would account for the fact that though the Tripsacum in western Guatemala is capable of surviving as a truly wild species, and in fact occurs as the dominant species in the vegetation over a rather large area, the Mexican teosintes have lost this ability and can persist only as weeds in and around the cornfields. Bukasov (1930) describes the teosinte of Mexico as a "dying out" weed.

Viewed from this standpoint the various colonies of Euchlaena in Mexico are seen, not as the result of a direct spread from the original colony which is probably the one in western Guatemala, but as the result of segregation from natural hybrids of maize and Euchlaena which the Indians unwittingly carried with them in the maize which accompanied them on their movements. The teosinte-like segregates which Collins and Kempton (1920) and Kempton (1924a) obtained from their crosses of Euchlaena and maize are ample evidence that this process may occur.

Final proof of these hypotheses must await cytogenetic studies of hybrids of the various forms of Euchlaena with a common maize parent, to determine whether the segments of Tripsacum chromatin are identical or different and are located on the same chromosomes. Another interesting line of evidence may be obtained by transferring these four translocation segments separately to early varieties of maize by repeated backcrossing followed by crossing of the separate strains to recombine the four segments into a single stock. Such a procedure should, theoretically, result in a new synthetic Euchlaena capable of maturing seed in the Northern states. These tests are mentioned only to show some of the numerous possibilities which are suggested by the various hypotheses proposed. It is scarcely necessary to add that some of these experiments are already in progress.

Only one important question remains. Which species of Tripsacum is the putative parent of the hybrid which gave rise to Euchlaena? The question is difficult to answer because the differentiation between the various species of Tripsacum is not clear-cut. The genus is in need of thorough revision by a competent taxonomist, a treatment which may prove to be difficult, for it is quite possible that the hybridization which resulted in the contamination of maize with the genes of Tripsacum has also resulted in a similar contamination of Tripsacum with maize genes. This may account, in fact, for the great variation found in the herbarium specimens of Tripsacum collected from Central America.

In spite of this confusion, however, several facts are obvious. The putative parent is not *T. dactyloides, T. floridanum or T. lanceolatum,* because none of these species possess all of the characteristics which are required in the putative parent and the last two are not found in Central America. There are three species of Tripsacum common to Central America—*T. laxum, T. latifolium,* and *T. pilosum*—any one of which in its general characteristics would qualify as the parent. The chief criterion which remains to be considered is the presence of secondary branches in the terminal inflorescence. Florida teosinte is outstanding in its characteristic of exhibiting a large percentage of secondary branches in the tassel, and this characteristic is one which is associated with the translocation segments from Tripsacum, as the data in Table 36 and Figure 78 show very conclusively. The Tripsacum parent of the hybrid must therefore have been a species in which secondary branching of the terminal inflorescence was common. Here again *T. dactyloides, T. floridanum,* and *T. lanceolatum* are immediately ruled out; and *T. latifolium* must be included in the same category. This leaves only two of the well-known species to be considered, *T. laxum* and *T. pilosum.* Examination of illustrations in the literature and of specimens in the herbarium of the Missouri Botanical Garden and the Gray Herbarium of Harvard University indicate that though secondary branches are found in both species, they are more common in *T. pilosum,* which has the most profusely branched terminal inflorescence of any of the recognized Tripsacum species. Thus, though the evidence so far available does not rule out *T. laxum,* it definitely favors *T. pilosum* as the putative parent and in any case eliminates the other species of Tripsacum from serious consideration.

It should be noted that all of the Central American species of Tripsacum which have been examined cytologically are autotetraploid. Since hybrids of diploid Zea and tetraploid Tripsacum are completely sterile, we must assume, (if Euchlaena is a hybrid of maize and *T. laxum* or *T. pilosum*) that hybridization occurred between tetraploid Zea and tetraploid Tripsacum, or that diploid forms of Tripsacum were in existence when the hybridization occurred.

So far as we are aware, Euchlaena is the only non-cultivated plant so far studied the origin of which can be traced to a completely domesticated cultivated plant; but the mechanism by which this change has come about is probably a very common one, more common, we believe, than has generally been realized. There are many partially fertile species hybrids in which the progeny exhibits an excess of parental types and a deficiency of intermediates. This is a natural consequence of the selective elimination of unbalanced chromosomal types and a selective survival of types resembling the parents. It is seldom, however, that the parental types recovered from such hybrids are identical with the parents themselves, for if hybridization is possible at all, there is usually, in the hybrid, some association of the chromosomes of the two species, and some opportunity for an exchange of chromatin is afforded. Many of the segregates resulting from such species crosses are therefore very likely to approach the parental types in their chromosome complexes, but some of the chromosomes are likely to have become infected with genes or chromatin segments from the other species. The transfer of the rust resistance of Yaroslav emmer to the common 21-chromosome wheats, to produce the rust-resistant Hope wheat (McFadden 1930) is a case in point. Hope wheat is a typical bread wheat except for its marked resistance to rust, a faint indication of emmer influence in the slightly fragile rachis, and its susceptibility to heat and drought. When Hope wheat is crossed with other wheats, the rust-resistant segregates which appear in later generations exhibit, almost without exception, some of these other characteristics which have been received from emmer. This indicates that Hope wheat differs from other common wheats not by one or two genes for rust resistance received from emmer, but by one or more short segments of chromatin all carrying emmer genes. Hope wheat is included here also as an example of how great an effect a single characteristic may have upon survival. Wheat is not now grown in the Gulf Coast region of

Texas and in many other parts of the South because the wheat rusts, *Puccinia graminis tritici* and *P. triticina*, overwinter there; infection takes place very early, sometimes in the fall, and because of the high atmospheric humidity develops rapidly and reaches epidemic proportions at an early stage of the wheat. The ordinary Mediterranean wheats of Texas do not survive in this region but typical Mediterranean-like wheats to which the genes for rust resistance from Hope (originally from emmer) have been added by hybridization are quite well adapted and have made yields approaching 30 bushels per acre. The single characteristic of resistance to rust has made almost all of the difference between complete extinction and a high degree of survival.

More nearly comparable perhaps are the natural hybrids of sorghum, *(Sorghum vulgare)* and Johnson grass *(Andropogon halepense)*. The latter is one of the most serious weeds in the South. Introduced into the United States about 1833, as a pasture and hay crop, it soon escaped from cultivation and in several generations has spread over the entire South and has become one of the most pernicious weeds in this region. Natural hybrids of sorghum and Johnson grass occasionally occur but are so rare that they usually are ignored in maintaining the purity of sorghum varieties. But during the recent years of severe drought in Kansas, the segregates from natural hybrids of Johnson grass with Atlas sorghum have increased to a point that plants with some of the characteristics of Johnson grass constitute a serious source of contamination in the crop*.

In this same connection we are informed by Dr. Sando† that in the cross of cultivated wheat with Agropyron, many segregates have appeared which would undoubtedly be capable of surviving and persisting in the wild.

The possibility of obtaining races with the chromosome number of one parent but with certain morphological features of the other has been demonstrated by Webber (1930). He obtained from a sequidiploid hybrid of *Nicotiana tabacum* ($n=24$) and *Nicotiana sylvestris* ($n=12$) segregates with 24 chromosomes, which resembled *N. tabacum*, but which possessed certain characters derived from *N. sylvestris*.

More recent investigations of Nicotiana hybrids by Avery (1938) have revealed a relationship between *N. alata* and *N. Langsdorffi* quite similar to that which exists between Zea and Euchlaena. Though the two species differ greatly in gross morphology, and to some extent in chromosome morphology, there is in the hybrids a regular chromosome conjugation and a high degree of fertility, indicating that "the distinctions between these two species in genic constitution and organization are not extensive." As in the case of Zea-Euchlaena hybrids (cf. Langham, 1938) many of the differences between the two species are inherited in a simple Mendelian fashion. Although there are differences in chromosome organization involving segments large enough to be visible, changes great enough to produce differentiation in external morphology have not destroyed the

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*From a conversation with Dr. John H. Parker.

†In a conversation.

homology of blocks of genes of sufficient length to insure chromosome conjugation and chiasma formation. Avery suggests that the pronounced distinctions between *alata* and *Langsdorffi* are not the result of a gradual accumulation of many gene differences, each with a slight effect upon characters of external morphology, but are more probably the result of Langsdorffi originating from a cross of a 9-paired ancestral stock with a race of *N. rustica* (n=24).

The actual mechanism by which blocks of genes may have been transferred from Tripsacum to Zea to produce Euchlaena, is nowhere better illustrated than in the studies of Anderson and Hubricht (1938) on hybridization in Tradescantia. These writers have presented evidence which indicates that when hybridization occurs in this genus, there is a common tendency for the hybrid to cross back to the more abundant species. The progeny of these secondary hybrids likewise cross back again to the parental species with the final result that a new form is developed which is almost indistinguishable in most of its characteristics from the more abundant parent, but which still shows definite evidence of an infiltration of germplasm from the other parent. This process is termed "introgressive" hybridization. Anderson and Hubricht have found definite evidence of strong introgression of *Tradescantia canaliculata* into *T. occidentalis* and of *T. canaliculata* into *T. bracteata.* In most of the populations studied the effect of introgressive hybridization was so overwhelming that the effects of other basic evolutionary factors, such as gene mutation, were completely obscured. Finally their analysis demonstrates that introgression is roughly proportional to the frequency of the introgressive species and that it is greater when plants are growing as weeds than when they occupy more natural habitats. They conclude that most of the introgressions in these populations have occurred in post-Columbian times and agree with Wiegand (1935) that natural hybridization is favored by influences, often man-made, which disturb the natural environment, tending to bring species which are ordinarily separated by geographical, ecological, or other barriers into propinquity with each other.

Here then, is a well established mechanism which accounts in all details for the development of teosinte from a natural cross of maize and Tripsacum. Of even more importance perhaps is the fact that it is probably an important mechanism involved in evolution in general, and one which has been too generally overlooked.

In spite of all the evidence which has been presented to show that Euchlaena is the product of the hybridization of Zea and Tripsacum, the fact remains that this conclusion is based entirely upon circumstantial evidence. We have no actual proof that such hybridization ever occurred in nature, and it is extremely doubtful whether it will be possible to synthesize teosinte from an artificial hybrid, although plants with some of the characteristics of teosinte are readily obtained. The fact that the evidence is largely circumstantial, however, does not render it valueless; for as Wiegand (1935) has pointed out, the classification of organisms is always based upon circumstantial evidence; no taxonomist has ever seen a species arise in nature.

The Place and Time of Origin

The only place in America where Euchlaena has been found growing as the dominant species is in the highlands of western Guatemala near San Antonio Huixta (cf. Kempton and Popenoe 1937). Not only does it grow in greater abundance and over a wider area in this region than in any other yet discovered in Central America or Mexico, but the strain found there is more Tripsacum-like than any other so far collected. Longley (1937) thinks that this form of Euchlaena shows slightly more admixture with maize than that from the Lake Retana region, but his evidence for this conclusion, the increased number of terminal knobs on the short arms of several of the chromosomes, suggests to us less rather than more relationship to maize; for as we shall point out later (page 262), it is quite possible that all the knobs of Euchlaena as well as those of North American maize varieties have been introduced originally from Tripsacum, some species of which have terminal knobs on almost every chromosome. In other characteristics, too, the Euchlaena from San Antonio Huixta appears to us to show less admixture with maize than any other form and it is, in our opinion, the original colony, resulting from the hybridization of Zea and Tripsacum, or if not the original, at least the nearest approach to this form so far discovered.

The evidence available on the time of origin is even less conclusive. In a previous paper (Mangelsdorf and Reeves 1938) we set forth some facts which suggested to us that Euchlaena had originated sometime after 600 A. D. (Spinden correlation), the date at which the Old Empire of the Mayas was abandoned. The basis for this suggestion is the fact that Euchlaena is unknown and Tripsacum is not abundant in the regions of the Old Maya Empire in Guatemala* or that of the New Empire in Yucatan. On the other hand, Euchlaena occurs in greatest abundance and Tripsacum also grows in profusion in a region in western Guatemala not far from the ruins of Quen Santos, where Seler (1901) discovered typical Maya monuments on which the earliest dates inscribed were identical with those found on the lintel at Chichen Itza, one of the important cities of the New Empire in Yucatan.

Furthermore, the region in which San Antonio Huixta is located is the only one yet discovered where the natives have for Euchlaena a word that is definitely of Maya origin. The name *salic* or *salicim* is a Jacaltecan word. According to Gates (1920) the Jacaltecan language is a branch of the Mame group of languages which are in turn related to the Cholti on the one hand and the North Maya and Quiché on the other. All are branches of the linguistic stock which Gates designates as "Mayance."

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*We have never visited Central America but this region has been the object of numerous botanical explorations. Our conclusions are based on the reports of Millspaugh, 1895; Millspaugh and Chase, 1903; Hitchcock, 1930; Standley, 1930, 1937; Bartlett, 1922; Swallen, 1934, 1936; Lundell, 1934, 1937.

Kempton and Popenoe (1937) suggest that the word *salic* may be an easy abbreviation of the word *salicim*, which probably has for its root the Maya word *ixim* for maize. In this region, then, and only in this region, is there a name for Euchlaena which is definitely Maya in its origin and one which suggests that the Mayas recognized the relationship of Euchlaena to maize.

Finally a sudden movement from the lowlands to the highlands of people accompanied by their corn varieties would afford unusual opportunities for the hybridization of maize and Tripsacum. Tripsacum is now, and probably was then, growing in great profusion on the hillsides; and it is conceivable that many fields of maize were surrounded by it. There is great likelihood, too, that the normal flowering habits of the maize would have been disturbed by the rather sudden change in altitude; that the normal tendency toward proterandry of the Central American maize would have been accentuated, so that the silks on many plants emerged only after the supply of maize pollen had been exhausted. If this occurred, there must have been literally thousands of opportunities for the natural hybridization of maize and Tripsacum.

We regarded all of these facts as suggesting, though by no means proving, that Euchlaena originated after the Mayas abandoned the Old Empire, some of them migrating to the highlands and bringing Zea and Tripsacum into direct contact with each other on a large scale.

Objection has been raised to these suggestions on the grounds (1) that the absence of Euchlaena in Eastern Guatemala and Yucatan is of no significance since there are many other regions where it is absent and (2) that there is no real evidence of a sudden migration from the lowlands to the highlands.

Admitting that these objections are quite valid, we still remain of the opinion that there is some significance in the fact that the largest known colony of Euchlaena, which is also the most Tripsacum-like Euchlaena, is found growing in a region where Tripsacum grows in great profusion, where some of the ruins are characterized by dated monuments, and where the natives have a Maya word for the plant. Perhaps additional data are needed before these facts can be properly interpreted. In the meantime, however, it is at least probable that the hybridization occurred before 900 A. D., for new types of corn which differ from those of the Andean region and which show evidence of contamination with Tripsacum made their appearance in the Southwestern Pueblo region at about that date, and are also found represented in the pre-historic Aztec pottery.

THE ORIGIN OF MAIZE

The Theoretical Nature of Primitive Corn

The new evidence on the origin of Euchlaena throws no direct light upon the problem of the origin of maize. It does, however, if accepted, eliminate from serious consideration all hypotheses which assign to teosinte any rôle in the origin of corn. Of the hypotheses which remain to be considered, the most simple, reasonable, and least taxing to our credulity is that the maize of today is a domesticated variation of a wild *Zea mays* which descended with Tripsacum, but along divergent lines, from a remote common ancestor, a conclusion which differs from Weatherwax's only in the fact that he has had Euchlaena also originating in this way.

What was the nature of this primitive wild corn from which the multitude of modern varieties has sprung? It must have been, in some respects, quite different from present-day corn; for the latter is not a plant adapted to survival in the wild. On the other hand, it need not have been as different as some students of the problem have supposed. It needed only two essential features which modern corn lacks—protection for the seed and a means of dispersal.

Imagination might devise any number of combinations of characteristics which would provide maize with these two essential features which it now lacks, but comparative morphology restricts the field to rather narrow limits. It suggests that dispersal was accomplished by a brittle rachis, as it is in certain forms of all other cereals (Vavilov 1926a) and as it is also in Tripsacum. It suggests that the seed was protected by the glumes, as it is in all other cereals and in practically all other grasses. Finally, comparative morphology suggests that present-day corn has had a perfect-flowered ancestor.

It so happens that we still have in maize a type which combines all of these characteristics—the well known pod corn, *Zea mays tunicata*, which is encountered as an impurity in some varieties, especially those of the Indians, and which is almost always included in the cultures of the maize geneticist. Many students of the problem, especially the earlier ones, were quite certain that pod corn was the primitive type from which domestic corn had descended, and in fact pod corn has often been known, particularly in popular parlance, as "wild" corn. For one reason or another, but primarily because the close relationship of maize and teosinte could not be ignored, more recent authorities have been inclined to dismiss pod corn as a possible prototype of modern corn. In view of the new evidence on the origin of Euchlaena, the time has come to re-evaluate the arguments for and against pod corn as a primitive type; and as there has been some misinterpretation of the early literature on the subject, a discussion of the history of pod corn appears to be in order.

History of Pod Corn

Sturtevant (1899) cites as the first reference to pod corn in the botanical literature a passage which appears in one of the old herbals, the *Theatri Botanica* of Gaspard Bauhin published in 1623. Here a corn, designated as *Frumentum indicum grano avellano magnitudine,* is described in terms which might well apply to pod corn, but which in certain respects are rather vague. Bauhin's account, which is photographically reproduced in Fig. 86, states that this corn is known in Africa as *manigette.* The name and descriptions are repeated, with modifications, in a number of the

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hoc frumenti genus, ſemper habuerunt, etiam ante Luſitanorum adventum: hiſt. Ind. Orient. part. 6. cap. 30.

An ſemen, quod Congiani Lucum vocant, cannabis grana, niſi quòd paulo ſit majus, referens, quod molâ manuariâ, ſubactum &piſtum, panem præbet candidum, tritico non inferiorem, hiſt. Ind. Orient. part. 1. l. 2. cap. 1.

an Arundinis genus granum ferens, noſtro Secali aut frumento ſimile, quod decoctum eſui eſt aptum: Inſulæ Virgineæ hiſtoria.

II. Frumentum Indicum grano avellanæ magnitudine.

Folia habet anguſta & tenuia, ſed in tantam altitudinem, quemadmodum tertium, non exurgit: ex ramis frumentum illud inſtar nucum avellanarum dependet, quod ariſtas habet cum Tritico ſive Mays convenientes, colore rubicundo: grana cute tenella involuta, putaminibus includuntur, & peculiaribus quaſi loculis, ad modum granorum in malo Punico, ab invicem diſtincta: ſeminatur in agris, quemadmodum frumentum verum, potiſsimum in Africa, & quidem in peculiari quodam loco, qui nomen etiam ſuum inde obtinuit: & Aethiopibus

Manigette; Batavis, Grain dicitur: part. 6. Ind. Or. cap. 38.

III. Frumentum Indicum Mays dictum.

an Triticum Bactrianum Plin. l. 18. c. 7.

Frumentum Arabicum, quod Mays nominant, in hiſt. Ind. Orient. part. 8.

Frumentum ex Guinea, ibid.

Triticum Indicum ſive Mays, quod Luſitani apud Nigritas primò ſeminarunt: in hiſt. Ind. Orient. part. 6. c. 31.

Pagatowr, Virgineæ indigenis.

Avati fructus, ex quo Braſiliani potum Kaawy coquunt: Stad. par. 3. Amer. c. 17.

Milium amplum, Triticum Sarracenicum, barbaris Avati, quod idem cum Indorum Mays, & Triticum Peruanum, Lerio part. 3. Amer. c. 8.

Milium Abrayn, id eſt, Siligo Turcica in Baly. par. 3. Ind. Or. c. 40.

Frumentum Aſiaticum: par. 7. Ind. Occid.

Milium Braſilianum: par. 3. Amer.

Milium in florida: par. 6. Ind. Occid.

Differentia notanda, cùm duo genera, ad ſex vel ſeptem pedes, tertium ad decem in Virginea excreſcat. Sic alterum craſsius & rotundius, ut quod è Lucanis tollitur: alterum ſubtilius & aridius, quod Morochen appellant.

Granum hoc magni prouentus eſt (bis enim Martio & Iunio ſerunt: part 2. Ind. Occid.) cùm in Peru ex vno grano 600. gignantur: at in Virginea mille & quinquaginta, & interdum bina millia reddat. Siquidem ſpica vel vna, vel binæ, ternæ, vel quaternæ, & ſingulæ ſpicæ quinquies, ſexies, & ſepties centena grana in Virginea contineant: apud Americanos, ſinguli culmi trib⁹ quatuorve ſpicis onuſti adoleſcũt, quarum ſingulæ, grana centum & amplius pendunt. Sic grana alba, rubra, flava, cærulea, in Virginea ſunt.

Frugum omnium communiſsimum Indiæ Occidentalis locis, in Peru, nova Hiſpania, Gutimala, Chile, & univerſa terra firma, in Inſulis verò non item: ſic & in Indiæ Orientalis aliquibus. Hoc Indi communiter cum prime commiſcent: & ex hoc ſolo panem Arepas nominatum, & potum Chicha (potus ſubacidulus Cici dictus: par. 9 Ind. Occid. addit.) Indis vocatum; ut fortiſsimum, quod in Peru Sora dicitur.

an hæc herba quâ in Braſilia aliquando ſenes virilia contegunt, cujus folia duorum digitorum latitudine, paulùm incurva, in longitudinem excreſcentia, veluti calamus qui ſpicam Milij ſive Tritici Sarracenici contegit: Leno in Braſil. cap. 7.

Hactenus ex hiſt. Indica: ſubijciamus recentiorum nomina.

Turcicum frumentum, Trag. (cui & Typha magna) Fuch.

Frumentum Indicum, Matth. Lon.

Milium Indicum Plinianum, Ruell. Geſ. Ad. Lob. cui & Mays Occidentalium.

Milium Indicum, Dod. (cui & frumentum Aſiaticum,) Tur. Lac. Geſ. cat.

Frumenti octava ſpecies Turcicũ dictum, Ang.

Triticum Bactrianum ſive Indicum, Cord. hiſt. Geſ. hor.

Frumentum Turcicum, Dod. Geſ. hor. (cui & Panicum peregrinum rectius,) Tab. Ger.

Triticum Indicum Fuchſij & Matth. Lugd.

Maizum, Monardj.

Maiz, triticum Indicum potius, quàm frumentum Turcicum dicendum, cùm non ex Aſia,

D ſed ſa-

Fig. 86. Reproduction of part of Bauhin's (1623) description of maize. His description of Form II was considered by Sturtevant to be the earliest description of pod corn. (Courtesy Harvard University.)

later herbals, all of which need not be mentioned here, for Sturtevant (1899) has presented a complete synonymy for this type of corn, and has included the references to the various authorities.

The next independent reference to pod corn in the literature, although it is not mentioned by that name, is that of Azara (1809). Azara was the Spanish commissioner and commandant of Paraguay from 1771 to 1801. Upon his return to Spain he completed a manuscript describing the country and its natural history. This was translated into French and published under the title, "Voyages dans L'Amérique Méridionale." On pages 146 to 148 in the chapter entitled "Des Végétaux cultivés," he describes four kinds of corn which he saw in Paraguay. One of these, known as "abatý-guaicurú," is certainly pod corn, for he states: ". . . chaque grain est enveloppé à part par de petites feuilles qui ressemblent entièrement aux grandes qui enveloppent l'épi éntier." There is no inference, as some writers have stated, that the corn grew wild; on the contrary, the fact that it is described in the chapter on "Des Végétaux cultivés" and not in the preceding chapter on "Des Végétaux sauvages" suggests quite forcefully that the plant was not a wild one. Nor is there any indication that this corn was grown by the Guaicurú Indians. It is designated "abatý-guaicurú" to distinguish it from "abatý-tý" or white maize.

The fourth kind of corn Azara describes as follows: "Je ne me rappelle pas le nom qu'on donne à la quatrième espèce, dont la tige, beaucoup plus mince, se termine, non par un épi, mais comme le millet, par une espèce de discipline à plusieurs cordes, dont chacune est couverté de grains absolument semblables à ceux du maïs, mais plus petits. J'ignore aussi les usages particuliers auxquels on peut l'appliquer. Je sais seulement qu'en faisant bouillir dans de la graisse ou de l'huile cette espèce de discipline qui contient les grains, ceux-ci crèvent tous sans se séparer, et qu'il en résulte un superbe bouquet, capable d'orner la nuit la tête d'une dame, . . ."

If this is corn at all, it is quite evidently, as Collins (1919b) has pointed out, a tassel-seed type. Weatherwax (1935) questions whether the plant is really maize and suggests that Azara might have been describing one of the species of Amaranthus, the small seeds of which are sometimes popped by heating in oil. The suggestion has some merit, for Azara does not mention Amaranthus, which is known to have been widely grown by the South American Indians (Safford 1917a); but there are several other widely grown South American plants which he does not mention, and so far as Amaranthus is concerned, Parodi (1935) does not consider it as one of the crops cultivated by the Guarany Indians. Azara's description of the terminal inflorescence as like millet might certainly refer to Amaranthus. On the other hand, it is almost equally possible that in comparing the inflorescence with millet he had in mind the sorghums which were, and are, frequently known as millet in both Spain and France. Weatherwax's suggestion that Azara may have been so far influenced by the food value of the plant as to have overlooked its natural affinities does not seem plausible. Although Azara would have been the first to admit his deficiency in botanical knowledge, for he begins his chapter on "Des Végétaux sauvages" with the statement, "Comme je ne suis pas botaniste . . . ," he was nevertheless a rather competent naturalist if we are to believe his biographer; and it seems improbable that he would have confused a monocotyledonous maize with so different a plant as Amaranthus. Again, his description of the grains as " . . . absolument semblables à ceux du maïs, . . ." certainly does not fit Amaranthus, although it does suggest some question in his mind whether the plant which he described was really maize.

In order to ascertain whether there are other plants grown by the South American Indians which might have been confused with maize, we have written Dr. Lorenzo Parodi, of Buenos Aires, one of the leading authorities on pre-Hispanic agriculture in South America, for his opinion on Azara's fourth kind of maize. He writes: "I presume that it is a sorghum. In Paraguay there exists a species of *Sorghum perennis* with a small ear (10 to 15 cm. long) with grains smaller than Kafir, that the scarcely civilized Indians cultivate even today.....You remember when Azara travelled through Argentina and Paraguay, around 1800, there was already considerable commerce between these countries and Europe and Africa. It is possible, then, that the plant alluded to was introduced by the Jesuits in their old missions."*

This appears to us to be a very reasonable interpretation. Azara himself mentions a number of Old World crops, including sugar cane and wheat, as among those grown in Paraguay at the time of his arrival; and Dr. P. C. Standley† informs us that in Central America, popped sorghum is used much more frequently than popped corn for confectionary purposes.

Despite this satisfactory explanation given by Parodi, and without reflecting in any way upon its soundness, we cannot refrain from adding one more hypothesis to those already considered. If the plant was really maize, it might well have been the homozygous or "earless" form of pod corn in which the stalk, frequently shorter than normal stalks, is terminated by a tassel, the branches of which are decidedly thickened as the result of the enlargement of the glumes, and which bear at the base, sometimes in profusion, small round or pointed seeds. Such a tassel might well be described as a "discipline à plusieurs cordes" and in fact Sconce (1912) applied a very similar description to the "earless" pod corn which appeared in his cultures: "Some tassels when gathered weigh as much as 2 pounds, having round kernels of corn hanging in festoons from the spikes of the tassel."

If pod corn was common in Paraguay, and apparently it was sufficiently common to be considered as one of the four types grown there, the homozygous or "earless" form must have arisen frequently and it may be that this is the form which Azara was attempting to describe.

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*Translated from Spanish.

†In a conversation with the senior author.

In any case he has presented a rather accurate description of this form, as can be readily seen by an examination of Figures 89-91, which illustrate the homozygous pod corn.

The next reference to pod corn appears in 1829 in Saint-Hilaire's letter to the French Academy of Sciences. Here for the first time it is designated as *Zea Maïs var. tunicata.* Saint-Hilaire had received the corn from the Abbé Damasio Larranhaga of Brazil who had sent a fragment of an ear of pod corn with the statement that it was cultivated by the Guaicurú Indians. Here again the earlier writers have been misquoted by more recent ones, for Saint-Hilaire makes it very clear that he does not believe this corn to have been grown by the Guaicurús and in fact insists that it could not have been, for these Indians were very primitive and were strangers to the art of tilling the soil. He states that the term "Guaicurú" is no more than a synonym for "sauvage" which may be interpreted to mean wild or primitive. Saint-Hilaire showed this ear to a young Guarany Indian whom he had brought with him to France and this young man who was born north of the state of Entre Rios in Paraguay acknowledged the maize as belonging to his country and stated that it grew there in the humid forests. As De Candolle later commented, "Comme preuve d'indigénat, c'est très insuffisant"; nevertheless Saint-Hilaire considered the evidence important enough to conclude that maize originated in Paraguay and that in the natural state the grains were covered with glumes as in pod corn, and like those of other grasses, and that these were lost following cultivation.

The next reference to pod corn, and the first illustration of this unique type (Fig. 87) appears in Bonafous' classical monograph "Histoire naturelle, agricole et economique du Maïs," published in 1836. Bonafous' pod corn, which he called *Zea cryptosperma,* was received from a French planter in South America, one M. Salgue, who evidently supplied very little information about the corn except to state that it was known as *pinsingallo* and that because of the difficulty of separating the grain from the glumes, it was grown but little. The statement that it was grown but little may imply that it was at least sometimes grown; but even more important is the name *pinsingallo* under which it was sent, for this word is undoubtedly a corruption or modification of the word *bisingallo,* which Dobrizhoffer (1822, first published 1784) used in connection with a kind of corn grown by the Guarany Indians of Paraguay. Dobrizhoffer, a Jesuit missionary to Paraguay from 1749 to 1767, in speaking of corn varieties, stated:

"The Guaranis sow various kinds of it. Those best known to me are the abati hatâ composed of very hard grains, the abati moroti, which consists of very soft and white ones, the abati mirî, which ripens in one month, but has very small dwarfish grains and bisingallo the most famous of all, the grains of which are angular and pointed."

The use of the expression "most famous of all" certainly indicates a type of corn quite different from the general run of corn varieties, and the description "angular and pointed" is an excellent description of the

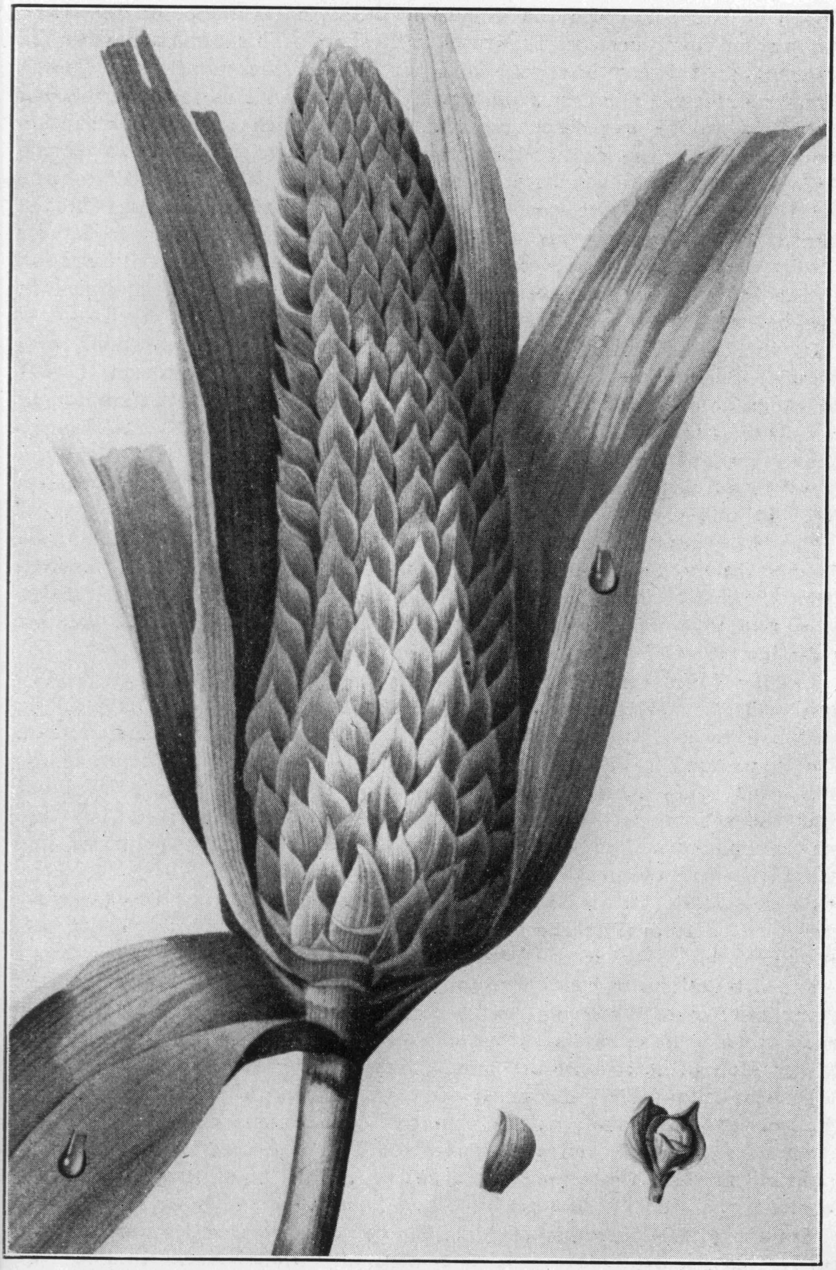

Fig. 87. The earliest printed illustration of the heterozygous form of pod corn. Reproduced from Bonafous 1836. (Courtesy Harvard University.)

grains of pod corn with the glumes attached, as a glance at Bonafous' illustration reproduced in Figure 87 will show. This combined with the resemblance between *bisingallo* and *pinsingallo,* the name under which Bonafous received pod corn from South America, leads us to the conclusion that Dobrizhoffer was describing pod corn, in which case his description should be counted as earlier than Azara's. However, if we are to include these indirect references to pod corn, there is probably one still earlier, for the Chinese illustration (Fig. 91) of corn which appears in the famous Pên ts'ao kang mu of Li Shih-Chen, which according to Laufer (1907) was published between 1560 and 1570, is an excellent illustration of the homozygous or earless form of pod corn, as the comparison in Fig. 91 or with Collins (1917, Plate 13A) will show.

In this category of possible references to pod corn we must also include the *Frumentum indicum alterum minus* of Parkinson (1640) which he describes as not having a crop "at the joynts of the stalkes, as the other, but at the toppes following the flowers." This, like Azara's fourth kind of corn and like Li Shih-Chen's illustration, is evidently a tassel-seeded type, and conceivably, if not probably, the homozygous earless form of pod corn.

The first mention of pod corn in an American publication is the description by Teschemacher (1842) of a sample of pod corn received from Texas. Because the single seed of this type which he planted gave rise to a naked-seeded plant, he concluded that pod corn was not a distinct species.

Lindley (1846) made a report to the Horticultural Society of London on a pod corn which had been sent to him by Mr. M. Fay of New York, who had received it from the Rocky Mountains as Native Indian corn. Fay considered it the original type of corn. Lindley who furnished the first good illustration comparing pod corn and naked corn pointed out that the cob or rachis of the naked corn was much larger than that of the pod corn, "as if the deterioration of the latter [glumes] had caused the enlargement of the former [cob]."

Salisbury(1848) called attention to the fact that pod corn was evidently composed of several subspecies for the seeds might be white, yellow, red, or purple.

An illustration of pod corn appears in the Annual Report of the Commissioner of Patents (1853) accompanied by the statement of an anonymous writer that this type of corn is found in a wild state in the Rocky Mountains and in the humid forests of Paraguay.

De Candolle (1855) discussed pod corn at length and concluded that the evidence that this was the primitive type was insufficient.

Sturtevant (1899) cites Klippart, 1858, as discussing pod corn in "Agriculture of Ohio," a reference which we have been unable to locate.

Darwin (1868) thought the fact that pod corn reverted to normal upon cultivation ruled out this type as a progenitor, but he did conclude that "It is almost certain that the original form would have had its grains thus protected." Carman mentioned pod corn in the Rural New Yorker in 1877. Sturtevant first mentioned it in 1879 and again in 1882. In 1883 he presented some data on the segregation of the podded character, and as Singleton (1935) has pointed out, these showed an association between the podded condition and sugary endosperm, thus anticipating by 36 years the linkage between the genes for these two characters which Jones and Gallastegui reported in 1919. In 1884 Sturtevant gave pod corn the name *vaginata* but he later returned to Saint-Hilaire's designation *tunicata*. This same paper has some excellent illustrations of pod corn. Sturtevant mentioned this type again briefly in 1885 and 1886, and again in two papers in 1894 in one of which he expressed for the first time the opinion that pod corn is a primitive type. His most comprehensive paper, the bulletin on "Varieties of Corn," published in 1899, discusses pod corn at considerable length and includes a list of the common names for pod corn which he had encountered: California corn, Cow corn, Egyptian corn, Forage corn, Husk corn, Oregon corn, Pod corn, Primitive corn, Rocky Mountain corn, in Africa *manigette*, and in Argentina *pinsingallo*. Sturtevant (1899) also stated that pod corn was illustrated in Landreth's seed catalog in 1889. We have not verified this particular reference but it is common knowledge that pod corn was for many years sold by seedsmen as a novelty. We have, however, found an illustration which Sturtevant apparently overlooked in Meehan's Monthly (1892) accompanied by a statement from an anonymous writer that "In this state [the podded condition] it is similar to any ordinary grass."

In the meantime several additional references to pod corn had appeared in European literature. Wittmack mentioned it in three papers, 1875, 1879, and (1880), and quotes a Professor von Radic of Serbia who obtained 125 podded ears and 102 naked ears in the progeny from a podded plant—another instance of a good Mendelian ratio in maize before the rediscovery of Mendel's law.

According to Wittmack (1880), Körnicke, 1872, in a paper which we have not had the opportunity to consult, recorded a case of normal corn reverting to pod corn, but Körnicke's statement that two of the three ears on this particular plant were normal while the other was podded is ample evidence that he was dealing with something other than pod corn. Two other cases of apparent reversion of naked corn to pod corn, reported by Sturtevant (1894) and Sconce (1912), can both be attributed to contamination by pod corn pollen; for there was a period when American seedsmen sold seed of pod corn as a novelty and it was widely grown in gardens.

Other early references to pod corn by Ascherson, Hackel, Körnicke and Werner, and Kellerman are given on pages 54 to 64.

It would be almost impossible to cite all the papers in which pod corn has been mentioned since 1900, for the tunicate character has been widely used in numerous genetic experiments and pod corn has been mentioned in almost every paper which has discussed the origin of corn.

Several papers which have appeared since 1900 should, however, be specifically mentioned in order to complete the history of pod corn. Blaringhem (1904) considered *Z. tunicata* a dominant variation and concluded that it was therefore of no significance in the ancestry of maize. Parker (1910) stated that pod corn is among the varieties grown by the Mohawk and Iroquois Indians and that the latter regarded it as sacred or original corn. East and Hayes (1911) presented the first data from controlled experiments which demonstrated that the podded condition is due to a single Mendelian factor. Collins (1917) first called attention to the fact that the homozygous podded form can usually be distinguished from the heterozygous, and that the former is frequently "earless" and bears perfect-flowered terminal inflorescences.

Pod corn as a Primitive Type

Here again it is teosinte and other extraneous considerations which have confused the picture. Saint-Hilaire did not question that pod corn was the prototype of cultivated corn; but later when pod corn was reported from such diverse regions as Paraguay and the Rocky Mountains, when it was discovered that it did not breed true but "reverted" to normal corn, and that it apparently arose spontaneously in the progeny of naked corn, many writers were led to dismiss it from consideration as the direct ancestor of modern maize. Finally when *Zea canina* was discovered and the close relationship of corn and teosinte demonstrated, pod corn was seldom again regarded as the prototype of cultivated corn.

Yet almost all students of the problem have endowed the hypothetical ancestor of corn with some, or all, of the characteristics of pod corn, and most of them appear to have had a feeling that it could not be ignored. De Candolle (1855) discussed it at considerable length. Darwin (1868) pointed out that the original form would have had its grains thus protected. Ascherson (1877) assumed that in wild corn the fruits were covered by husks as in pod corn, but he considered the husks of pod corn to be monstrosities. Körnicke and Werner (1885) thought that pod corn had the ear characteristics of wild corn but that it could not be the original corn because it does not breed true. Kellerman (1895) considered that original corn had individual husks on the kernels and that these disappeared when the husks surrounding the entire ear developed.

Sturtevant (1894) was one of the few later students who succeeded in ignoring teosinte, for he wrote: "From a botanical standpoint I am disposed to accept *Zea tunicata* as a primitive form from which are derived *Zea everta*, the pop corns; *Zea indurata*, the flint corns; *Zea indentata*, the dent corn; *Zea amylacea*, the soft corns; *Zea saccharata*, the sweet corns; and *Zea amyleasaccharata*, the starchy-sweet corns," and again, "We hence are inclined to believe that when a truly wild *Zea* is discovered it will be of podded form, the kernels small and very flinty."

Montgomery (1906) assumed that the ancestral form was a perfect flowered grass with terminal inflorescences. East and Hayes (1911) in speaking of pod corn state, "It is probable that the prototype of the species possessed this character." Later East (1913) spoke of a "towering prince of grasses" having tiny seeds developed from perfect flowers on loose terminal spikes. Collins (1912) realized that pod corn must be fitted into the picture; "that the prototype of maize should be sought in a grass possessing the peculiar characteristics of *Zea tunicata*"; and again, "The definite tendency toward a brittle rachis in podded plants and the demonstration that this character may serve as a natural means of dissemination, are additional evidence that the podded varieties of maize are not meaningless monstrosities, but definite reversions to a perfect-flowered ancestor." And still again (1917), ". . . in every particular by which *Z. tunicata* departs from normal maize, it does so by replacing the specialized characters of maize with characters common to practically all other grasses." But Collins could not ignore teosinte and so arrived at a compromise in which he had maize originating from a hybrid of teosinte and an unknown pod-corn-like plant. Weatherwax (1935) assumed that primitive corn had the seeds partially enclosed in bracts but he did not call this pod corn.

After compiling this review of the conclusions of so many competent students, we obviously can make no claim to originality in suggesting that pod corn is the primitive type; the prototype of modern corn. Whatever contribution we may make to the solution of the problem lies (1) in eliminating Euchlaena from further consideration, and (2) in emphasizing the fact that it is not the familiar heterozygous, segregating, form of pod corn which is to be regarded as the primitive type, but the homozygous, true breeding, earless form which bears its seeds in the terminal inflorescence.

All of the evidence from comparative morphology suggests that cultivated maize had in its ancestry a perfect-flowered plant having covered seeds on a terminal inflorescence, with brittle branches. Many students of the problem have endowed the hypothetical ancestor with some or all of these characteristics. Why look further for the hypothetical ancestor of maize when in pure pod corn we already have at hand a plant which meets all the requirements?

All of the considerations which have stood in the way of reaching this conclusion are now removed. De Candolle was apparently concerned about pod corn being reported from such diverse sources as Paraguay and the Rocky Mountains. This is easily explained, for it is frequently found in Indian varieties. Darwin and later writers could not believe that a primitive type would revert so easily, but modern genetic studies have demonstrated that he was speaking of the heterozygous type. Blaringhem's assumption—that it has no significance in the ancestry of maize, because the character is dominant or progressive—should carry no weight with geneticists. The apparent cases of the spontaneous appearance of the podded condition in normal corn—reported by Körnicke, Sturtevant, and Sconce—can all be attributed to pollen contamination or other causes.

And the final obstacle, the necessity of fitting Euchlaena into the picture, has been removed by the data which indicate that this genus is the progeny rather than the prototype of maize.

For final proof of the hypothesis we could ask for only one more bit of evidence, the actual discovery of pod corn growing in the wild. We shall show later that even this evidence may be forthcoming when we begin to seek wild corn in the proper place, and when we begin to search, not for some strange grass that botanists have never seen, except in their imaginations, but for an earless, small-seeded plant not greatly different from the homozygous pod corn found in the cultures of maize geneticists.

The Change from Pod Corn to Modern Corn

Since a naked-seeded corn would not have survived long in nature, and since the adoption of agriculture by primitive man was probably not a sudden event but a gradual process, we may assume that the first corn to be domesticated was a wild pod corn. Once corn came under man's ministrations it probably began almost immediately to vary in new directions and even before the mutation from covered seeds to naked seeds occurred, new varieties of pod corn considerably different from the original wild corn had already come into existence.

But the most important and far-reaching differences between wild pod corn and modern cultivated varieties are those resulting from the change from covered seeds to naked seeds. This change was the consequence of a single gene mutation from the dominant *Tu* to the recessive *tu*, a mutation which may have occurred repeatedly in the past history of the plant, only to be lost in nature, where such a variation was decidedly deleterious. Once the mutation occurred under domestication, however, where it was beneficial, it immediately acquired a survival value which it had not previously possessed. This situation is not at all unusual. Dobzhansky (1937) cites a number of instances in which a mutation with a deleterious effect under one set of conditions became advantageous under a different set. And Parodi (1938) has concluded that most of the changes occurring under domestication are the result of selection of characteristics which are deleterious to a plant growing in the wild but beneficial to a plant existing in a man-made environment.

The objection will no doubt be raised that a primitive wild plant does not become a highly specialized cultivated plant as the result of a single recessive mutation. This is obviously true. On the other hand recessive variations have played a very prominent part in the development of many of our cultivated plants (cf. Vavilov 1926a, 1927) and some of these have had profound effects. Several of the so-called subspecies of maize differ from each other primarily by single gene mutations. The flint corns, *Zea indurata*, for example, differ from the flour corns, *Zea amylacea;* and the sugar corns, *Zea saccharata*, differ from the non-sugary types, *indurata*, *indentata*, *amylacea*, and *everta*, primarily by single genes.

Nevertheless it would be a mistake to assume that the mutation from

Tu to *tu*, important though it has been, is responsible for all of the differences between wild pod corn and modern cultivated corn. The pod corn found occasionally as a mixture in modern cultivated varieties is certainly not the wild pod corn which the wandering Indians discovered millennia ago. Modern pod corn is the result of superimposing a single "wild" gene with perhaps a few closely linked modifiers upon a genetic complex which has been tremendously altered by centuries of domestication. Although there is, so far as we know, only one *Tu* gene, the expression of this gene varies tremendously with the substratum upon which it is superimposed, so that there could, theoretically, be as many different kinds of pod corn as there are distinct varieties of naked corn (Fig. 88). All would be identical however, in certain important characteristics always associated with the *Tu* gene; glume-enclosed seeds, a brittle rachis, and a tendency for the homozygous form to be earless and polygamous or perfect-flowered.

Fig. 88. Variation in the glumes of heterozygous pod corn from those which scarcely cover the seeds (left) to those which are virtually monstrosities (right). This variation is probably the result of superimposing the *Tu* gene upon widely different substrata, although it is also possible that different alleles of *Tu* are involved.

Consequently we visualize wild pod corn as identical with modern pod corn only in possessing the *Tu* gene and the characteristics always associated with it but differing from it in a large proportion of the remaining genes. Modern naked-seeded varieties, on the other hand, differ from the original wild pod corn not only in lacking the *Tu* gene but also in many other genes as well. The differences may be illustrated by assigning simple gene symbols to the three types:

Wild pod corn —$TuTu\ AA\ BB\ CC \ldots XX$
Modern pod corn —$\left.\begin{matrix}TuTu\\ Tutu\end{matrix}\right\} A_1A_1\ B_1B_1\ C_1C_1 \ldots X_1X_1$
Modern naked-seeded corn—$tutu\ A_1A_1\ B_1B_1\ C_1C_1 \ldots X_1X_1$

In what other characteristics wild pod corn may have differed from modern corn we have no way of determining but there are good reasons for making certain rather definite assumptions. Wild corn was probably a hardier plant than modern cultivated corn. The culms were probably shorter and more slender. The seeds undoubtedly were no larger than was necessary to supply an abundance of food to the embryo, and corneous enough to resist insects and decay. We may assume that the seeds were sharply pointed, for even today, when the podded characteristic is superimposed upon modern varieties, there is a tendency for the seeds to become pointed as a result of the pressure of the glumes. Most of these features are characteristic of some of our modern pop-corn varieties, such as Rice Pop, and although the latter is probably, as we shall show later, a recent development, there is reason to believe that the seeds of wild corn were capable of popping. We suspect, in fact, that primitive man first discovered the value of maize as a food plant when the accidental application of heat caused the seeds to burst from their enveloping glumes, thus converting an inaccessible, stony seed into a very promising and palatable food.

Our assumptions regarding the nature of the seeds of wild corn are in agreement with those of Sturtevant (1894) who stated that he regarded pop-corn as a primitive type, though he gave no reasons for this conclusion.

If the effect produced by the *Tu* gene in the homozygous state, when superimposed upon modern varieties, is a criterion, we may conclude that the inflorescences of wild pod corn were mainly terminal. If lateral inflorescences occurred at all they were probably not enclosed by leaf sheaths, and were, like the lateral inflorescences of Tripsacum, quite similar to the terminal one.

When the mutation from pod corn to naked corn first occurred under domestication it brought other important changes in its wake. Not only were the glumes surrounding the seed reduced to inconspicuous bracts but —if again the behavior of the *Tu* gene in modern cultures is a criterion— there was an increased tendency toward the development of lateral inflorescences and toward the separation of the staminate and pistillate spikelets, so that the terminal inflorescence became predominately staminate, the lateral ones pistillate.

As a result of these changes natural selection began to operate in new directions. There was a shortening in the axis of the lateral inflorescence or an increase in the length and number of the leaf sheaths, or both, which eventually brought about the present complete covering by the husks. Mrs. Kellerman (1895) has already described this process: "These branches became shortened and form the shank or footstalk of our present corn. The shortening of the branches brought the sheaths close together, thus forming the husk or general protective envelope of the ear. When the general envelope was provided the individual 'husks' [as in pod corn] were no longer produced." This, we believe, is a good description of what has taken place, except that instead of having the individual "husks" disappear because they were no longer necessary, we would have the individual husks or glumes lost by a single recessive mutation, and the husks over the ear appearing, not in response to necessity in the Lamarckian sense, but because variations in this direction had now acquired a survival value which they had previously not possessed. This conception differs, too, from that of Weatherwax (1935), who visualizes the change as a reduction of the bracts accompanied by a complete sheathing of the ear by the husks, two gradual processes occurring simultaneously. We see the first occurring abruptly as a single gene mutation and the second following gradually as a consequence of the change produced by the first. In either case, however, modern corn has acquired genes for the pronounced development of lateral leaf sheaths which wild corn did not possess, so that the addition of the gene for poddedness to the modern genetic complex results in the anomalous situation of caryopses twice protected, once by glumes surrounding every grain, again by husks surrounding the entire ear. It is not at all surprising that some botanists have regarded pod corn as a monstrosity.

Survival of the *Tu* Gene: We first thought to account for the presence of pod corn in modern varieties as the result of reverse dominant mutations. Mutations of this kind do occur. Karper's (1932) studies of the dominant tall mutation in sorghum furnish an excellent example of a cultivated recessive returning to its original dominant form. And though Collins (1919b) speaks of pod corn's having arisen more than once by mutation from non-podded varieties, we can find no evidence that this has ever occurred in historical times. True Körnicke, Sturtevant (two cases), and Sconce have reported its spontaneous appearance in non-podded corn, but Körnicke's case is eliminated by his own description and the remaining cases are easily accounted for as the result of pollen contamination.

Within the past twenty years literally millions of plants of thousands of inbred strains of corn have been grown under controlled conditions, and no one, so far as we are aware, has ever observed a change from naked corn to pod corn in these pedigreed cultures, though other gene changes, some of them dominant, have been noted. Even the extensive experiments with X-rays which have increased the mutation rate tremendously, and which have, in some cases, produced dominant or progressive mutations, have brought forth no pod corn. Thus until pod corn has been shown to arise spontaneously, we may conclude that the podded gene of today is a "wild" gene which has been transmitted through generations of domestication as an impurity or "rogue." This is not an unreasonable assumption. Pod corn is not uncommon among Indian varieties and most Indian tribes were notoriously negligent in maintaining purity in their corn varieties. In the absence of human selection against the podded condition, its frequency in the population would have changed but slowly, for as Haldane (1932) has shown, selection pressures are relatively ineffective when gene frequencies are very high or very low. In the absence of rigid human selection against the podded gene, natural selection probably at times acted in its favor even when corn was grown under domestication. Sturtevant (1894) cites a correspondent who observed a gradual increase in the proportion of podded ears in a stock of Blount's Prolific and also (1899) mentions a year in which his entire collection of corn with the exception of the pod corns was destroyed by insects. Collins (1912) mentions an instance of pod corn volunteering in an experimental field in Maryland where it had been grown the previous year. If these were common occurrences in aboriginal agriculture, the gene for poddedness might have been maintained in the population almost indefinitely.

All of these facts considered, it does not seem unreasonable to suppose that the pod corn in existence today is partly, if not wholly, a survival of the original wild gene. If this is the case, it represents a gene which has existed for thousands of years almost exclusively in the heterozygous condition. This would account for some of its present characteristics, particularly its frequent sterility when homozygous, for Muller (1918) and others have shown that a constant state of enforced heterozygosity is one of the surest means of accumulating deleterious recessives. Continuous heterozygosity may also account for the accumulation of modifiers which have increased the length of the glumes until today they are as long in the heterozygous condition as they probably were originally in the homozygous state, with the result that homozygosity in modern corn brings forth glumes which are developed to the point of monstrosities. Weatherwax (1935) may be quite right in his opinion that in primitive corn the glumes were not as long as they are in present-day pod corn. But this does not rule out pod corn as the primitive type, for we must not overlook the fact that the expression of the podded gene and its immediate modifiers as well as the genetic background of hundreds of unrelated genes, upon which it is expressed, have both been tremendously altered by centuries of domestication.

True-breeding Pod Corn

In its homozygous condition pod corn is frequently sterile. Seed production is scanty and sometimes fails completely; anthers frequently fail to dehisce and sometimes are decidedly aborted. So far as we are aware modern pod corn has never been propagated in pure form. Consequently one of the most frequent objections that we have encountered to the recent revival of the hypothesis that pod corn is a primitive type is that cultivated corn could scarcely have descended from a sterile form. We have never considered this objection a particularly formidable one, for we should have expected that any character which had been maintained for hundreds or thousands of years in a heterozygous condition would be decidedly abnormal when reduced to the homozygous state. Furthermore, as we have already pointed out, the pod corn of today is probably the result of superimposing a single, wild, relic gene upon a substratum quite different from that upon which it expressed itself in nature. Finally we have been convinced that by selection of modifying factors it would still be possible to obtain a true-breeding pod corn with a high degree of fertility, for the essential factors for fertility are already present. Accordingly we began in the spring of 1938 to select for increased fertility in the homozygous form. This was obtained even more easily than we had expected, for in a population segregating for *Tu* and Ts_5, the latter a dominant gene for tassel seeds, the earless types classified as homozygous pod were highly fertile and set seed in abundance. Open-pollinated seeds from this type grown in the summer of 1938 produced only *Tu* plants, proving that the parent plants had been correctly classified.

Since the marked fertility of the parent plants was not noted until after seed had set and blooming had long since ceased, it was not known whether the plants were also fertile on the staminate side; but in the succeeding generation all of the homozygous earless types exhibited normal anthers filled with apparently normal pollen, and all tassels which were permitted to remain on the plants produced functional pollen. Self-pollination was impossible, for anthesis did not occur until after the silks had lost their receptivity, but sib pollinations between homozygous plants can probably be made by utilizing several successive plantings of the same stock. Unless still other factors are involved it should be possible to produce a stock in which the *Tu* gene can be propagated in the homozygous condition indefinitely.

The dominant gene Ts_5 is apparently an important modifier of fertility of the homozygous form of pod corn. Whether it was such a modifier in the wild is problematical. In any case the homozygous combination of *Tu* and Ts_5 *is* highly fertile and, more interesting still, is very similar to Tripsacum in several botanical characteristics (Figs. 89-90). The branches of the tassel bear staminate spikelets above and pistillate below, with an occasional perfect flowered spikelet usually found in the region where the staminate and pistillate spikelets merge. The chief characteristic in which the plant differs from Tripsacum is in its glumes, which are membranous rather than horny. In this form, maize, which is usually considered one of the most highly specialized grasses, is actually less advanced in specialization than Tripsacum.

This homozygous, earless form of pod corn would probably be capable of surviving in the wild under the proper conditions. Its seeds are protected by prominent glumes, and a means of dispersal is provided by the fragile rachis which breaks apart quite readily. Whether the branches of the tassels are actually more brittle than those of normal maize is not certain. The rachis of the ear of pod corn is definitely more brittle and disarticulates more readily than the cob of normal corn, and there is an indication that this is also true in the rachises of the tassel. In any case there is no doubt that the tassel branches are fragile enough so that the seeds

Fig. 89. The terminal inflorescence of a fertile homozygous form of pod corn. The "arching" is often characteristic of this form at this stage. Note the resemblance of this form to the Chinese drawing in Fig. 91. Note also that it fits Azara's description (p. 224) of the fourth kind of corn observed in Paraguay.

Fig. 90. Fertile terminal inflorescences of homozygous pod corn. Note the similarity of these inflorescences to those of Tripsacum in having staminate spikelets above; pistillate spikelets below.

which are borne on the branches are readily disseminated when the plant is mature. There is a tendency for the tassel to break, not at every joint as does Tripsacum, but in small pieces to which two to a dozen seeds are attached. This method of dispersal, in the wild, would have resulted in groups or clumps of seedlings emerging in one spot. It seems quite possible that the Indians originally adopted the hill method of corn culture because maize was found growing thus in the wild.

The homozygous podded plants are always shorter in stature than normal plants or heterozygous podded plants in the same culture. They bear a striking resemblance to the early Chinese illustration of Li Shih-Chên, as is shown in Fig. 91, where the two are directly compared. They answer also to Parkinson's description of *Frumentum indicum alterum minus* and to Azara's description of the fourth kind of maize grown in Paraguay in which the stalk is terminated by a "discipline à plusieurs cordes." It is quite possible that if the seeds on these tassels were small and corneous and

Fig. 91. The earliest Chinese illustration of maize which appeared in the *Pên ts'ao kang mu* of Li Shih-Chen about 1560-70. (Reproduced from Bonafous 1836). Although the drawing is obviously somewhat conventionalized it shows a remarkable resemblance to the fertile homozygous form of pod corn with which it is compared. It is quite possible that the Chinese drawing is intended to illustrate the homozygous pod corn which might well have been introduced into China through India by the Spanish and Portuguese, who were exploring South America at the same time that they carried on extensive trade with the East.

capable of popping, heating the entire tassel in oil would result in the "superbe boquet" which Azara describes. Attempts to produce such a type by repeated backcrossing with pop corn are now in progress.

Possibility of Producing a Synthetic "Wild" Corn

Unless wild corn is still in existence, and we shall show later that this is a possibility, the nearest approach that we can make to it would be a "synthetic" wild corn. It should be possible to produce this by removing from teosinte, through repeated backcrossing, the translocation segments originally from Tripsacum, which distinguish it from maize. This process should result in a naked type of maize with many "wild" genes in its genetic complex, not the same genes, perhaps, that characterized the original wild corn, but genes quite similar in their effects. By superimposing upon this complex, through repeated backcrossing, the gene for poddedness, we should have a plant quite similar in its essential features to the primitive wild corn; a plant which would probably be quite capable of perpetuating itself in nature at least in those regions where teosinte now grows as a wild plant.

Place of Origin of Maize

The Primary Center of Domestication*

In determining the center of origin of cultivated plants the evidence from distribution, wild relatives, history, archaeology, linguistics, and other sources is usually considered. In the case of maize there has been, up to the present time, a very definite and, perhaps, justifiable tendency to lay the greatest stress upon the occurrence of wild relatives, and hence to seek the center of origin in a region where these occur. For many years this line of reasoning has pointed to Mexico where teosinte is a common weed in and around the cornfields. But with the recent discovery of teosinte as a truly wild species in Guatemala, the scene has shifted from the Aztec tablelands of Mexico to the Maya highlands of western Guatemala (Kempton and Popenoe 1937).

If we dismiss teosinte as a recent development having no part in the origin of maize, there remains no necessity for seeking the center of origin either in Mexico or Central America. As a matter of fact, paradoxical though it may appear at first glance, the new evidence on the origin of teosinte as a hybrid of Zea and Tripsacum suggests that we seek the center of origin of maize or at least the primary center of domestication in a region where its relatives do *not* occur. The reasoning is simple. Though natural hybridization of Zea and Tripsacum is undoubtedly rare, and though there is no evidence that it has occurred more than once, yet if hybridization is possible and the two genera have

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*We are using the term "primary center of domestication" to designate the region where maize first reached a high degree of specialization as a cultivated plant. The initial domestication of the wild plant may, however, have occurred in a contiguous region, as will be shown later.

been growing in the same habitat for thousands of years, hybridization might have occurred again and again, especially in earlier periods before the two genera had become as widely differentiated as they are now. Had this happened, we should expect to find in existence a series of species or genera intermediate in some of their characteristics between Zea and Tripsacum. The fact that there is only one, Euchlaena, and that this one is apparently a very recent addition to the tribe, suggests that the opportunities for hybridization have been restricted to relatively recent times when the ranges of Zea and Tripsacum have been caused to overlap as the result of man's migrations.

There are many areas in the world where Tripsacum and Euchlaena do not occur, but only one that merits serious consideration as the center of origin of maize as a highly-specialized cultivated plant—the Andean region of South America. Teosinte is unknown there, and though Tripsacum has been reported from Ecuador and Bolivia (Hitchcock 1927), it has never been discovered in Peru (cf. Macbride 1936) and its occurrence in Bolivia and Ecuador is certainly sporadic and may, like that of Coix, be the result of a post-Columbian introduction.

Aside from the question of wild relatives, most of the remaining evidence has for many years pointed to the Andean region as the primary center of domestication. This evidence now becomes quite acceptable, and need no longer be dismissed with unsatisfactory explanations.

Sturtevant considered that the large, soft-seeded Cuzco type of corn represents the greatest departure from the primitive condition and that its occurrence in Peru pointed to a South American origin of maize. At the same time, however, he considered the presence of *Zea canina* with its small hard seeds as an indication of the Mexican origin of corn. It has since been shown that *Zea canina* is a hybrid having no bearing on the problem.

Vavilov (1926a, b, 1927, 1931a, b, 1932a, b), who has probably given more consideration to the study of the origins of cultivated plants than any other writer since De Candolle, has suggested several criteria for determining the center of origin. One of these is the amount of diversity; the center of origin, according to Vavilov, should be sought in that region where the greatest diversity occurs. De Candolle (1855) had called attention to the greater variability of domesticated plants in their region of origin, but Vavilov more than any other writer has made use of this characteristic to determine centers of origin. His hypothesis is based on the assumption that in the distribution of any cultivated plant, only samples of the existing diversity are carried to new regions so that the greatest diversity always remains at the center—an assumption that has been strengthened by Wright's (1931) mathematical studies of evolution in Mendelian populations. There are obviously many factors which might vitiate this hypothesis but in general it has proved to be a very fruitful one.

If we apply this formula to maize we can reach but one conclusion—that the center of origin is in the Andean region, for as Collins (1931) has stated: ". . . the region that includes Peru, Bolivia, and Ecuador can show a greater diversity of maize types than the whole North American continent." Kempton (1926) had previously expressed a similar opinion: ". . . the greatest specialization of the plant occurs in Peru—and were it not for the absence of close relatives in South America the botanist unhesitatingly would give credit for the domestication of this plant to the Incas or their predecessors."

Strangely enough, Vavilov (1931a) reaches a different conclusion, for he assigns the center of origin to Central America and Mexico. It is evident, however, that Vavilov's conclusion is based not alone on the amount of diversity in the two regions; Collins is undoubtedly correct in attributing a greater diversity to the Andean region than to any other and Kuleshov's (1933) data on the Russian collection of world corn varieties tend to support his statement. Vavilov, apparently, as so many who preceded him, found it impossible to ignore the presence of teosinte in Mexico and its absence in Peru and after assigning the center of origin to the former, felt compelled to explain the great diversity in the latter as the result of the widespread practice of irrigation.

Another of Vavilov's criteria for determing the centers of origin of cultivated crops, the frequency of dominant genes, also points to the Andean region as the home of maize. Vavilov (1927) has shown that in the case of Secale, Hordeum, Avena, Cicer, Vicia, and other genera, there is a decrease in dominant types from the center of origin to the periphery of spread. This is due primarily to two factors; one is the "emancipation" of recessive genes in the original population, a vague but rather apt term to describe the normal course of evolution in Mendelian populations which become separated into small groups, a process which has been treated mathematically by Wright and clearly described by Dobzhansky. The second factor is the frequency with which cultivated plants become differentiated from their wild progenitors as the result of recessive gene changes, some of which would not survive in nature in a homozygous condition. There may be still other factors involved in the distribution of dominant and recessive genes, but in any case it appears to be an excellent criterion for distinguishing the center of dispersal from the periphery.

The application of this criterion to maize yields the same results as does the previous one, and points again to the Andean region as the center of origin. Kuleshov (1933) has mentioned the very dark, dense anthocyanin pigmentation on plants of Peruvian corn, and no one who has ever examined a Peruvian collection of maize varieties could fail to be impressed by the frequency of various dominant endosperm, aleurone, and pericarp colors. Pure white corn is rare in Peru in relation to the colored types, and perhaps it is for this reason that the *maiz blanco* is regarded as the "noblest of all cereals" (Squier 1877).

Through the kindness of Dr. R. A. Emerson we have had the opportunity of examining the seed of the 336 lots of South American corn collected some years ago by the late Dr. Erwin Baur. In the entire collection there were only 59 white-seeded varieties. All others exhibited one or more dominant endosperm, aleurone, or pericarp colors and in the case of the latter an extensive series of multiple allelemorphs.

The exact source of many of the lots in this collection is now unknown, but a comparison of the frequency of white-seeded types in those from known sources is interesting. The frequency by countries is as follows:

Country	*Total No.*	*No. White*
Peru	61	5
Bolivia	100	14
Ecuador	48	18
Colombia	6	2

The percentage of pure white varieties in Bolivia is almost twice as high and in Ecuador approximately four times as high as in Peru.

It is unfortunate that we do not have similar collections from Mexico and Central America for direct comparison. We have had, however, over a period of years, the opportunity to observe a rather large number of Mexican varieties and we have never been impressed by an absence of white-seeded varieties or a great frequency of the colored types, and Kuleshov (1930) states that three-fourths of the Mexican dent corns are white and that the dent corns predominate in Mexico. True, the dominant aleurone, endosperm, and pericarp colors are frequently encountered in all Indian corn and there is probably not a single dominant character in Peruvian corn which does not occur occasionally in North American corn. The great difference, however, lies in the frequency with which pure dominant types are encountered in Peru as compared to other parts of America.

Linguistic evidence throws but little light on the problem of the center of origin, although it does indicate that corn was carried to the West Indies and perhaps to Florida from South America. It is of no help, however, in deciding between Central and South America as the center of origin. Both regions have their own names for the plant and there is no apparent relationship between the names in the two regions. Archaeological evidence, except that which bears upon the question of the origin of teosinte, has been of but little more value. Maize was the basis of culture and civilization in both regions, but there is no direct evidence to tell which one first made use of it. True, there are many features of the Peruvian culture which indicate a greater age than that of the Central American ones, and recent investigations are beginning to disclose signs of a South American influence upon the earlier Central American cultures, but in general the archaeological evidence on this point is not clear-cut. It is perhaps of some interest that the Peruvians, though they had many ceremonies connected with the planting and harvesting of maize, and though they fully realized its importance in their economy, had no myths or legends regarding its origin, as did many other American peoples. This may suggest that they had possessed corn for so long that it was taken for granted, or it may merely mean that they were less disposed to speculate about it.

It is also a fact that in Peru among the living forms, the plant remains, the stone and clay replicas, and the representations found on the pottery, a series of maize ears can be found illustrating many of the steps which we assume to have occurred since wild corn was first domesticated, while similar material found in other regions illustrates only well-developed forms. It can be said, therefore, that the archaeological evidence has favored slightly a South American origin of maize and, at least, has contradicted in no essential way the evidence from other sources which points to the Andean region.

Prehistoric Pod Corn in Peru: As usual, one discrepancy must arise to mar the picture. We have assumed that the original wild corn which was put into cultivation by man was a pod corn and that our present naked seeded types have come about as the result of a mutation which occurred during domestication. Next we have presented evidence that the primary center of domestication was in the Andean region. Yet this region is one of the few places in America where pod corn is unknown. Collins (1917) states that O. F. Cook, who made a special inquiry for this type of maize in Peru, found no knowledge of it, nor any words for it in the extensive Quichua vocabulary of words related to maize. Collins also states that pod corn has never been found in Mexico, but a more recent paper by Khankhoje (1930) indicates that it does sometimes occur there.

This discrepancy yields to a rather simple interpretation, for upon further consideration we are inclined to conclude that we should not expect to find pod corn in Peru at the present time. Certainly the wild form will never be encountered there, for the Peruvians long ago had made use of every square foot of land adapted to agriculture; and the better soils, those particularly adapted to maintaining maize in the wild, would have been occupied very early. The first corn grown as an agricultural crop in Peru was either the primitive pod corn or a partially domesticated, naked-seeded maize, from the lowlands, not far removed from the primitive pod corn and still showing occasional tunicate plants as rogues. In the first eventuality the primitive pod corn became differentiated into many varieties in the numerous separated valleys, not so much as the result of human selection but as a consequence of the natural course of evolution in Mendelian populations separated by geological, ecological, or other barriers. The mutation from pod corn to naked corn may have occurred in only one of these valleys, and as the merits of the new type became recognized, it spread gradually from one valley to another where it hybridized with the native pod corn cultivated in each one. In many valleys the new naked corn was not immediately adapted and became so only after repeated back-crossing with the native corn. Thus there was a period when the corn in any one locality was a mixture of the local pod corn and the new naked corn. The same general situation would have obtained if domestication, and the mutation from pod corn to naked corn had first occurred in the lowlands. In either case pod corn may have persisted as a rogue for a long period of time, perhaps for centuries. But once the Indians became more skilled and began to practice rigid selection against the podded type, it must soon have disappeared. The Peruvians at the time of the conquest had made greater progress in the art of agriculture than had any other American people, and though we need not endow them with superlative skill as plant breeders, it is not too much to assume that they had acquired sufficient experience to propagate from types which suited their needs or fancy and to discard those which failed to meet these requirements. And though, as we have already indicated, the podded gene would have persisted almost indefinitely if the selection pressure against it were slight, it would have disappeared from the population very rapidly if selection against it had become rigid. If podded seeds were never planted, and podded plants produced no more pollen than normal plants, the frequency of the podded gene would be reduced by half in each generation. And if rogueing of podded plants before pollen was shed was ever practised, the podded character might theoretically have been exterminated in a single year.

Seen thus, the presence or absence of pod corn in aboriginal varieties is one measure of the Indians' proficiency in agriculture. Pod corn is not found in Peru and is rare in Mexico and Central America, because agriculture in both of these regions is very old and highly developed. The Indians in these regions had become skilled husbandmen, and the podded character had been eliminated by rigid selection. But in the lowlands of South America and among the less settled tribes of North America, agriculture remained more primitive; selection against the podded condition was not rigid, and the gene for poddedness still survives.

If this rather involved assumption is a sound one, we might expect primitive podded types to be represented in some of the earlier Peruvian pottery, for the art of pottery-making often follows soon after the art of agriculture is acquired, and the Peruvians who were very realistic in many of their representations would certainly have reproduced pod corn if it were common.

Accordingly we began a search for representations of pod corn in the prehistoric Peruvian pottery in the museums and in the numerous illustrations which appear in the American and European literature on South America archaeology. For months the only approach to a pod-corn-like ear which could be found was the stone replica illustrated by Squier. Harshberger once described this as a "bad" drawing; but since the vase shown on the same page, and taken from the same grave, is well-drawn, as are most of the other illustrations in the book, it seems more likely that the replica, rather than the drawing, is a poor one. In either case, however, the ear, though showing some resemblance to pod corn, shows not quite enough resemblance to be considered as conclusive evidence.

We had almost concluded that our hypothesis was not a sound one, or that it would need to be modified by the additional assumption that pod corn had disappeared from Peru before the art of pottery making had reached a stage of making accurate representations of food plants, when a visit to the Peabody Museum of Yale University by the senior writer led to the discovery of a beautiful representation of a prehistoric ear of primitive Peruvian pod corn, in the exhibit of the Yale Peruvian Expedition. This ear, photographs of which are reproduced here (Fig. 92) through the kindness of Dr. Cornelius Osgood, anthropologist of the Peabody Museum at Yale, was collected, according to the notes in the catalog, in the Inca highlands of Peru. Examination shows that it is made of clay and that it is not, like many of the very accurate representations in the Peruvian pottery, a cast. Each kernel has apparently been laboriously shaped and placed in its proper position on the ear, so that the kernels in their glumes overlap like the shingles on a roof. The replica is so faithful that the position of the kernels within the glumes can in some cases be determined. Another replica, in this same collection, the one shown on the left in Figure 15, may also be a representation of pod corn, although this is by no means as certain as it is in the case of the ear illustrated in Figure 92.

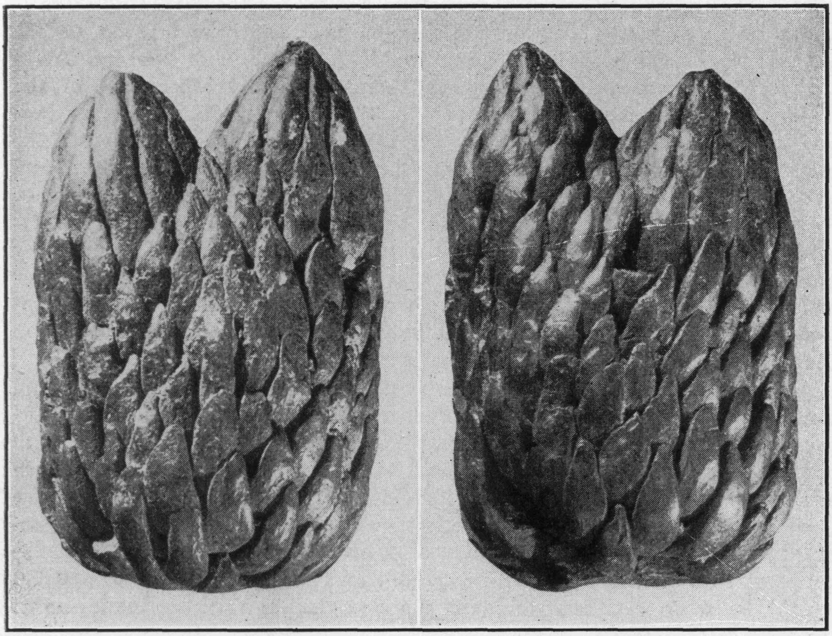

Fig. 92. Two views of a pre-historic replica of pod corn from highlands of Peru. Natural size. (Courtesy Peabody Museum, Yale University.)

Since we had predicted, on hypothetical grounds, that representations of pod corn would be found in prehistoric Peruvian pottery, even though pod corn is not known in Peru today, the actual discovery of an almost perfect replica of this type, together with one or two others that may be pod corn, is strong evidence that the hypothesis is a sound one.

The Probable Native Habitat of Wild Corn

Though the Andean region is undoubtedly the primary center of domestication of maize, it does not follow that corn originated there as a wild species. In fact, it seems quite probable that it did not. Maize is essentially a tropical or sub-tropical, moisture-loving plant with a marked preference for fertile soils. Even with a certain hardiness which has presumably been lost through domestication, maize would have been rather exacting in its requirements and there are not many regions in America where it would have persisted indefinitely as a wild plant.

The preference for fertile soils suggests alluvial or prairie regions; the lack of resistance to cold or drought suggests warm, humid zones, while the easily broken dormancy suggests a climatic region where rainfall is abundant during growth, but lacking after the grain has reached maturity—an alternation of rainy and dry seasons.

A plant with these requirements would not have been found growing wild in the coastal valleys of the western Andes, for there rainfall is rare, many of the streams are intermittent in their flow, and much of the natural vegetation is watered almost wholly by fogs. It is even less likely that corn originated in the Titicaca basin or in any other part of the inter-Andean plateau, for its culture in this region is hazardous at best and as a crop it has been largely replaced by potatoes and quinoa. The eastern slopes of the Andes are more favorable as a natural habitat and in the Urabamba valley, it is true, occurs the greatest development of maize varieties. In this region, too, the great Inca civilization had its center and here agriculture reached a higher pinnacle than in any other part of America. Rainfall, however, is not too abundant in the upper slopes of the eastern valleys and much of the corn is grown under irrigation. It is very doubtful whether maize would have been found growing in the wild in a region where irrigation is required for its culture. We must, it appears, go still farther east for its native habitat, to the warm humid zones of the valley floors, where numerous alluvial fans, formed by countless streams descending from the valleys of the Eastern Cordillera, are bordered by the forests; or better still to the rainy-green savannas which are scattered throughout the forested lowlands. Here, we believe, is the ideal home for wild maize, a perfect combination of climatic and geographic features, fertile soils, reasonably high temperatures, and an abundance of rain during the growing season, followed by a dry period during which the seeds can reach maturity and maintain their dormancy until the next rainy season begins.*

In many respects corn is a typical Amazonian plant. It has many of the characteristics which Weberbauer (1936) lists as common to the plants of the tropical rain forests, including pendulous leaves, colored foliage, long aerial roots, a cauliflorous inflorescence, small flowers without conspicuous coloring, and a tendency toward a separation of the sexes in the flowers. Yet it does not seem possible that corn could have been

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*For geographic descriptions of the Andean region and other parts of South America, see Means (1936), Bowman (1916), Weberbauer (1936), and Whitbeck (1926).

a rain-forest species, for it competes but poorly with other plants and would not long survive in the tangled vegetation of the tropical forests. Furthermore, its mechanism for the maintenance of dormancy is not at all well developed and in the humid forests the seeds would be almost viviparous, germinating before they had been disseminated.

Scattered through the Montaña, however, are typical xerophytic formations and the rain forests are constantly merging with the rainy-green savannas. In the Southern lowlands of Brazil, in the Paraná-Paraguay basin, for example, only one-third of the land is in forest, the remainder in grassland. Yet the rainfall is abundant—50 to 60 inches annually—with a distinct dry season from May to September. This means an abundance of rain during the growing season and a dry period during which the seed can remain dormant until the next growing season begins.

With the conception of corn as a native of the tropical lowlands of South America, the historical evidence on pod corn acquires a new significance. There are four independent references in the historical literature, already reviewed, which associate pod corn with the Guarany Indians or with the region which they occupied, a region which includes all of Paraguay and parts of Uruguay, Argentina, Brazil, and Bolivia (cf. Métraux 1928). Let us review this evidence briefly: Azara (1809) described as one of the varieties grown by the Guaranies of Paraguay, a form which was undoubtedly the heterozygous pod corn and another which may well have been the homozygous "earless" form. Saint-Hilaire (1829) received pod corn from Brazil and it was identified by a Guarany in France as belonging to his country. Bonafous (1836) received pod corn from Argentina, another Guarany region, under the name *pinsingallo.* A half century before, Dobrizhoffer, 1784, had described under the name *bisingallo* a "most famous" kind of corn grown by the Guaranies of Paraguay, in terms which leave little doubt that he was also describing pod corn. Finally, Payne (1892), who had read widely in the literature of the early explorers, tells us that "The Jesuit missionaries, following aboriginal tradition, always considered this [the River Plate Basin] to be the original seat of maize-agriculture and the tunicated maize of Paraguay to be the original form of the corn."

Here, then, are five items of evidence all pointing in one direction. Considered independently they are meaningless, except to show that pod corn was known in South America. Considered together and combined with the evidence that pod corn is a primitive type, and that the adjoining Andean region, apparently the primary center of extensive domestication, possessed pod corn in earlier times, they constitute a body of circumstantial evidence which cannot be ignored.

Various derivatives of the word *bisingallo* still persist in regions formerly occupied by the Guaranies. Parodi (1935) lists the words *pisingallo, passankalla, pisincho* and *pisinga* which he states are applied to varieties with "granos pequeños, duros y acuminados, que se emplean para freir." Granado (1931) describes from Bolivia a *Maiz piksenkella* the grains of which are "delgado, menudo blanco, empleado para tostado, que revienta al cocerse como rosa, presentando un aspecto simpático." This comparison of the burst corn with a rose is curiously reminiscent of Azara's description of the fourth kind of corn, which upon cooking results in "un superbe bouquet, capable d'orner la nuit la tête d'une dame."

It is evident that these recent South American writers are describing a small, hard-seeded type of corn which is used for popping. We have already suggested that the wild pod corn was of this nature, and that its usefulness may have been discovered when the accidental application of heat caused some of the grains to burst out of their enveloping glumes. There is no indication that the types of corn described by Parodi and Granado are pod corn, but it seems possible that various derivatives of the word *pinsingallo*, which we know from Bonafous' statement was at one time applied to pod corn, are still applied to corn that has some of the characteristics of the original primitive corn, for example small, hard seeds capable of popping. This is merely a suggestion; we refer the word *bisingallo* and its numerous progeny to the linguists for further study.

The prevalence of pod corn in the lowlands of South America would account for its appearance in every other part of the world where it has been found. The rivers in the lowland adjoining Peru and Bolivia serve as so many natural avenues of approach to the upper slopes of the Andes, and since the Andean region obtained its mandioc, sweet potatoes, and several other important crop plants from the lowlands, it is not difficult to imagine that maize travelled the same paths.

The Spanish-employed explorer Sebastian Cabot sailed up the Paraná-Paraguay river in 1527 nearly a century before the landing of the Pilgrims in Massachusetts. The city of Asuncion was founded in Paraguay in 1535. At the same time the Spaniards and Portuguese were carrying on extensive trade with Africa and India. If pod corn was common in Paraguay at the time, and we know that it was still being grown by the Guaranies when Azara resided there at the close of the eighteenth century, it would not be at all strange if some of it were spread to Africa and India and from there through Tibet into China, which as Laufer (1907) has shown is the path by which maize reached China. Therefore, it is not surprising to find Bauhin reporting pod corn from Africa in 1623 or to find an illustration of what appears to be the earless pod corn appearing in the Chinese literature of the sixteenth century.

All of this suggests that the search for wild corn should be directed to the lowlands of Paraguay, Northeastern Bolivia, or Southwestern Brazil. If it grew at all in the valleys of Peru it has probably long since disappeared, for all the available sites which might have served as a natural habitat for wild corn were put into cultivation at an early date. Perhaps the possibilities of finding wild corn even in the lowlands are not too great. The plant probably was already restricted in its habitat when man arrived on the scene. His depredations in earlier stages, when he harvested maize only in the wild, probably reduced the population still further. Even after agriculture was invented and maize was maintained artificially, there may have been repeated onslaughts on the wild crop in seasons when the cultivated fields failed. The introduction of cattle and other grazing animals by the Europeans has not improved the plant's chances of survival, for most herbivorous domestic animals prefer the succulent growing maize plant to almost any other vegetation. Considering all these facts, we can be reasonably certain that maize is nowhere growing in great profusion as a wild plant. But knowing where to search for it, and knowing in a general way the kind of plant for which to seek, there is at least a remote possibility that we may yet discover, in protected sites, in the still unexplored lowlands of Paraguay, Bolivia, or Southwestern Brazil, small colonies of the wild pod corn from which our modern maize has descended.*

Secondary Centers of Domestication

Vavilov (1926a) has shown that there is sometimes, in addition to the primary center of domestication, a secondary center, where hybridization has given rise to new forms. This appears to be the case with maize, for in Mexico and Central America there exist great opportunities for the hybridization of maize and teosinte and there occur many types of maize which might have originated from such crossing.

Teosinte is not widespread in Mexico and Central America, but there are localities where it occurs in great abundance. At Huipulco in Central Mexico, Bukasov (1930) found it occurring as a weed in the corn fields constituting up to 30 per cent of the plants in the fields. In the Southern part of the Valley of Mexico where it is known as *acece*, which means "small cobs falling asunder," it comprised 10-15 per cent of the plants in the field. A considerable part of the teosinte gathered in Mexico appears to contain natural hybrids and at Atoyac and Coyoacan, intermediate specimens were noted which local inhabitants stated were of frequent occurrence and which were harvested and used for feeding poultry. It is a common opinion in Mexico that these hybrids eventually revert to pure corn or pure teosinte.

This hybridization has presumably been occurring for centuries, and since the hybrids of teosinte and maize are highly fertile, with regular pairing of the chromosomes and free crossing over of maize and teosinte chromosomes, it is almost certain that new types of corn must have arisen from the process. This accounts, we suspect, for the great diversity of maize in Mexico and Central America. It accounts, too, for the fact that this region, though second only to the Andean region in varietal diversity, exhibits a diversity of quite a different type from that found in the Andes, for while it lacks many of the Andean types, it possesses others which the Andean region has never known.

Peru is noted for its great diversity of the *amylacea* or flour corns, which Kuleshov considers the most ancient type; and these are almost lacking in Central America and Mexico except in one area in the central

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*Since the above was written, we have had communications from several botanical collectors in South America, which indicate that primitive corn has been until recently, and may still be, in existence in Paraguay.

tablelands (Kuleshov 1930). On the other hand three of the five main groups of corn—*indurata*, *everta*, and *indentata*—are found in greater diversity in Central America and Mexico than in the Andean region, a fact which coupled with the presence of teosinte compelled Bukasov (1930) to conclude that this region, rather than the Andean, is the primary center of origin of maize.

Instead of regarding the presence of teosinte and the diversity of varieties in Mexico and Central America as evidence that this region is the primary center of domestication, we regard the first as the cause of the second. Seen from this viewpoint the diversity in the Andean region becomes still more significant, for there it is primarily the product of a long period of domestication, while in Mexico and Central America it is the result of hybridization.

New Types of Maize Originating from Hybridization With Teosinte

The Pointed Pop Corns: If we assume that maize came originally from South America, there are several new types which we should, on *a priori* grounds, expect to have resulted from contamination with Tripsacum by way of Euchlaena. One of these is the pointed-seeded pop corn of the White Rice type. This type would be expected because both Euchlaena and Tripsacum have small, hard, pointed seeds and many of the segregates obtained from teosinte-maize hybrids also have small, hard, pointed seeds. In fact *Zea canina*, which later was shown to be a hybrid of maize and Euchlaena, received its name from the fact that its seeds were decidedly pointed. Furthermore it is possible to isolate pop corn strains from a cross of maize and Euchlaena. Some years ago Dr. Kuleshov in a conversation with the senior writer suggested that pop corn had originated in this way. Having available at the time an F_2 of a cross of dent corn and Florida teosinte, we selected small, pointed-seeded types, tested their popping expansion, and in several generations isolated a new pop corn variety which from the standpoint of popping expansion was quite satisfactory, but which was later discarded because of susceptibility to smut.

Knowing that small, hard, pointed-seeded types would be expected from crossing of maize and Euchlaena; knowing that this type of pop corn has actually been obtained from such a cross; and knowing that the pointed-seeded pop corns occur in Mexico in greater diversity of form and color than in all of the remainder of the world combined (Kuleshov 1933), we feel that it is not too much to assume that they are the result of hybridizing South American corn with Euchlaena. Furthermore Rice pop corn possesses certain genetic peculiarities which are found in some varieties of teosinte or segregates from maize-teosinte hybrids, including marked cross sterility (Demerec 1929) and a deficiency of sugary seeds in hybrids with sugary endosperm (cf. Emerson 1924, 1934, Mangelsdorf and Jones, 1925).

It now becomes necessary to make a distinction between the pointed pop corn of Mexico and other parts of North America and that of Peru. We have assumed that the original wild pod corn possessed small, hard, pointed seeds capable of popping. When the gene for poddedness was lost through mutation, this type should have been similar, so far as the seeds are concerned, to the Rice pop of Mexico. We have also assumed, however, that this pointed-seeded pop of South America, being one of the earliest types developed under domestication, was no longer in existence, for it was never shown in replicas or representations on the pottery, although a form which we assumed to represent the state immediately succeeding the pointed pop, a small-eared type with slightly larger, softer, pointed seeds is frequently encountered in the Andean region, both in living specimens and replicas. In fact Knowlton's so-called fossil ear was of this type.

Recently, however, Kempton has published an illustration of a small-eared, pointed pop corn from Peru which fulfills almost exactly the mental description, which we had formulated on hypothetical grounds, of the primitive type of corn which must have been in existence soon after domestication had begun, the podded character had been lost, and the lateral branches had disappeared. In spite of the fact that the seeds of the Peruvian pop are quite similar to those of the North American pop, the two types are quite different in other respects, and are readily distinguished (cf. Kempton 1937, Plate 10). Even more different than their appearance is their theoretical phylogeny, for the Peruvian pop corn is primitive because it has never departed widely from the original wild corn, while the North American pointed pop is primitive because some of the "wild" characteristics lost through domestication have been restored by hybridization with Euchlaena, which presumably received these characteristics originally from Tripsacum.

The Dent Corns: Another type of corn common in Mexico is dent corn. Kuleshov (1933) states that approximately three-fourths of the Mexican varieties are dent, and he regards Mexico as the center of diversity of this type. For some reason the dent corns are almost unknown in the Andean region, and those which are encountered there today are usually, and quite obviously, recent North American introductions. Jones (1924) has shown that dent types may originate from hybridization of pop corn and flour corn, and we suspect that the Mexican dents have originated in this way. If so, they represent a secondary product of hybridization of maize and Euchlaena.

Flour corn is not widespread in Mexico, but it is abundant in limited areas of the central tablelands. Kuleshov (1930) thinks that an interpretation of this spot of flour corn, so far removed from the center in the Andean region, would go far toward explaining the migrations of maize. The interpretation may be a very simple one, for flour corn, because it is easily masticated or ground, is preferred by primitive people in any region where it can be grown. In tropical regions where insects constitute a hazard, or in cold regions where the grains of flour corn, when planted, are likely to mold and decay at the prevailing low soil temperatures, the flint corns being harder persist, in spite of an inherent preference for soft corn.

If the migration of maize from South America to North America was a gradual process, then the corn which first reached North America must have been a tropical flint corn, for no other type could have spread through the equatorial regions. As cooler elevated regions in Mexico were reached, however, where insects were not such a serious hazard, the flour types, which differ from the flint types primarily by a single gene, would again have been isolated just as they were originally in the Andean region. If this is true the soft corn of the Mexican tablelands represents a secondary center of soft corn wholly independent of the Andean center.

When the pop corns, originating by the hybridization of tropical flint and Euchlaena, later crossed with the flour corns of Central Mexico, some dent types must have occurred; and these being more suitable for human consumption than either the flint or pop corns, but adapted to regions where the flour corns were not suitable, probably spread widely through Mexico and other regions. In fact the dent corns of the Southern United States are undoubtedly predominantly of the Mexican dent type, for a number of the modern Cotton-Belt varieties can still be duplicated by Mexican varieties. Furthermore it is known that the dent corns were present in the South at an early date, for Gilmore (1931) has found dent corn among the plant remains of the Bluff-Dwellers in the Ozarks. And Beverly in 1705 (cf. Carrier 1923) describes the so-called "She-corn" of Virginia as "shrivell'd with a Dent in the Back of the Grain, as if it had never come to Perfection."

The direct spread of dent corns from their center of origin in Mexico to South America, however, met an effective barrier in the tropical regions, so that the dent corns found in South America today are, at least for the most part, post-Columbian introductions.

The modern dent corns of the Corn-Belt represent still a different line of descent and are a comparatively recent, post-Columbian development. Wallace and Bressman (1928) have presented evidence that this type is the product of crossing the Southern gourd-seed, itself a Mexican dent type, with the Northern flint. At any rate it is known that these two distinct types were grown by early settlers and were sometimes mixed, and it is common knowledge that types resembling both putative parents may be isolated from Corn-Belt dent varieties.

This may represent a case of adjusting the percentage of Tripsacum "blood" to suit particular conditions, the Southern dents possessing not enough, the Northern flints too much. In any case modern Corn-Belt dent varieties appear to be intermediate between the gourd-seed type and the Northern flints in the amount of Tripsacum infection which they exhibit.

The Tropical Flint Corns: The original flint corn introduced from South America was probably a small-seeded form with the large cobs and irregular rows of grain characteristic of most of the prehistoric Andean corn.

Crossing of this type with Euchlaena produced the pointed pop corns and subsequent backcrossing of the pop corns with the tropical flints led to the development of new types of flint corn previously not in existence. These new types, possessing corneous seeds, were, in contrast to the dents, capable of spreading southward through the tropics, and this accounts, we believe, for the fact that Central America exhibits a greater diversity of flint corn types than any other part of America. It also accounts for the fact that the flint corn grown in almost all parts of South America except the Andean region shows evidence of contamination with Tripsacum.

Crossing with Euchlaena not only introduced new diversity and an opportunity for many distinct new forms to develop, but it brought into maize new genes, originally from Tripsacum, for resistance to heat, drought, and cold, and perhaps for resistance to insects and diseases.

Tripsacum is, in many characteristics, an extremely hardy plant. True, it does not survive well under conditions of severe grazing or in fields under cultivation, but it has a wide range of adaptability so far as soil relationships are concerned. Once established it thrives upon almost any type of soil, and is found both in marshy situations and on dry, rocky hillsides. Tripsacum is resistant alike to heat, to drought, and to extreme cold and is comparatively free from attacks of insects and diseases. Therefore it is not at all surprising that the incorporation of some of the hardiness of Tripsacum into maize should result in new types of corn better adapted to many regions, particularly those where agricultural practices were primitive; and it is not surprising that most of the corn of northern South America is quite similar to that of Central America in exhibiting characteristics of Tripsacum. That these new types did not replace the old even in the Andean region is probably due to the fact that corn had been domesticated for so long and had become so well adapted there, that even the improvement brought about through the addition of Tripsacum germplasm did not render the new types superior to the old for these particular conditions. Furthermore the increased hardiness resulting from Tripsacum infection was not so essential in the Andean region where agriculture was highly advanced and where irrigation was a common practice.

The Southwestern Flint and Flour Corns: Other effects of crossing South American corn with Euchlaena, which we might have expected on *a priori* grounds, are lengthening of the ear and straightening of the rows of grain. Most prehistoric Andean varieties have large misshapen cobs and many rows of corn arranged in such an irregular fashion that it is almost impossible, in many ears, to count the rows. The Andean ear of corn is truly a counterpart of the central spike of the tassel which is also polystichous and in which the spikelets appear to be arranged almost wholly at random.

In crosses of corn and Euchlaena two types appear regularly (Fig. 75) in which the ears are long and the rows very straight and distinctly separated in pairs. It is not improbable that repeated hybridization of an irregular-rowed type of corn with Euchlaena would result in new types with straight rows. Such an effect is seen in the Mexican dents and the tropical flints of Central America and South America, which are frequently long and straight-rowed when compared with Andean varieties. It reaches its maximum expression, however, in the long, slender, straight-rowed flint and flour corns of the Pueblo region of the Southwestern United States. Since these types are not known in Mexico, we can assume that they are an indigenous development in the Pueblo region, which must, therefore, be regarded as a tertiary center of formation of new types.

To understand how these new forms may have come into existence, it is necessary to review the sequence of maize types which occurred in this region. From the descriptions of Kidder and Guernsey (1919) and from a study of specimens on exhibition in various museums, particularly the Peabody Museum of Harvard University, it is evident that three distinct types of corn have occurred in this region. The first culture period associated with maize, Basket-Maker II, exhibits only the large-cobbed, small-seeded, irregular-rowed tropical flint which is quite similar to some of the prehistoric Andean types. In the next stage known as Pueblo I the Mexican dent types appear and included among these are branched ears quite similar to the famous branched corn of Tuxtla, Mexico, described by Collins and Doyle (1911). The long, slender, straight-rowed types which characterize the region today and modified forms which are common throughout the Northern United States do not make their appearance until the stage known as Pueblo II, which is reached about 900 A. D.

Exactly how these new types may have originated is impossible to determine; but since they exhibit even more Tripsacum influence than the Mexican dents, which were already present, and since the pointed pop corns also make their appearance on the Southwestern scene at about the same time, it may be assumed that the straight-rowed flint corns are the product of crossing the local dents, originally from Mexico, with the pointed pops, also from Mexico. The same result, however, might have come about through another hybridization of the dent corns with Euchlaena, and the fact that the Indian varieties from this region have an abnormal chromosome 10, identical with that found in Chapingo teosinte (Longley 1937), might be regarded as evidence for this view. Also some of the prehistoric cobs found in the museums are quite similar to types appearing among segregates from maize-teosinte hybrids. But whether they originated from a direct cross with teosinte or are a secondary product resulting from a cross with the pointed pop, it is a fact that they exhibit a much greater influence of Tripsacum than do the Mexican dent corns. Many of the Southwestern varieties tiller very freely, and in general appearance of the plant are almost indistinguishable from the segregates of maize-teosinte hybrids. Jones, Singleton, and Curtis (1935) have shown that tillers are correlated with higher yields in early-maturing varieties, the tillers apparently acting as a supplement to the main stalk in the manufacture of food. This being true, it is quite likely that genes for tillering originally from Tripsacum, but introduced into maize from

Euchlaena, were more likely to be retained in northern than in southern corns. In any case the freely-tillering flint corns of New England with their long, straight-rowed ears are not essentially different from the long, straight-rowed varieties of the Pueblo region. In the latter, however, flour types have also developed, which would be expected since they are preferred for food and are easily grown there, and undoubtedly recur frequently as the result of single gene mutations.

The Sweet Corns: The sweet corn of commerce apparently originated in New England. At any rate the first reference to it appears in the New England Homestead in 1822 and Bement (1853) states that sweet corn was introduced into Massachusetts in 1779 by Capt. Richard Bagnel, who was a member of General Sullivan's expedition.

"Sugar or sweet" corn is listed in Thorburn's Seed Catalog in 1828 and the first illustration occurs in Bonafous' monograph in 1836, where it is designated as *rugosa.*

Sweet corn was, however, fairly common among Indian tribes in North America; Maximilian found the Mandans growing it in 1833 (cf. Atkinson and Wilson 1915) and Will and Hyde (1917) list, as possessing sweet corn, the following tribes: Hidatsas, Mandans, Omahas, Pawnees, Ponkas, and Iroquois. These writers cite Boller as stating that the Indians of the upper Missouri never picked true sweet corn for roasting ears, using field corn instead for this purpose; and Erwin (1934) has reached the conclusion that sweet corn has never been particularly prized by the Indians in North America. This is apparently true also in South America, for though sweet corn is grown in Peru (cf. Herrere 1921), and was known in pre-historic times (cf. Hendry 1930), it is not used for roasting ears even today.

There are, as in the case of several other main types of corn, two distinct forms of sweet corn, the North American and South American. Sturtevant clearly recognized the differences between the two and called the former, the true sweet corns, *saccharata,* and the latter, the starchy-sweet corns, *amyleasaccharata.* We have recently discovered (unpublished) some genetic differences between the two types. A sweet corn, closely resembling the *amyleasaccharata* type of Peru, isolated from a Texas variety with Mexican dent ancestry, has proved to be the result of an *su* gene which is not identical with the *su* gene of Northern sweet corn, but is allelic to it and is dependent upon another gene in the tenth chromosome for its expression. We suspect that this is the same type which Bukasov found in Mexico, for Sturtevant reported the starchy-sweet type from that country. It may also be the same type found by Freeman (1915) in Arizona. At any rate, until its relationship to Peruvian sweet corn has been determined, we are designating it as Mexican sugar to distinguish it from the Andean sugar of Peru which presumably has never been contaminated with Tripsacum and the North American sugar of the Northern states which shows a pronounced Tripsacum influence.

Other Differences Between Pure Maize and Tripsacum-Infected Maize

Frequently encountered in North American corn are numerous characteristics not yet mentioned, which may trace their origin to Tripsacum. One of these is the great difference in proterandry between North American and Andean types. The former are usually slightly proterandrous, anthesis occurring several days before the silks appear; a few varieties are proterogynous, the silks emerging before pollen is shed. But the Andean varieties have such a pronounced proterandry, at least when grown in North America or Europe, that it is sometimes impossible to effect self-fertilization. Kuleshov (1933) has called attention to this fact and mentions that in some samples the silks did not appear until two or three weeks after anthesis.

Tripsacum, on the other hand, is always strongly proterogynous, the silks on a particular inflorescence emerging and losing all receptivity long before anthesis occurs on the same inflorescence. If the North American types have originated from the hybridization of the Andean types with Tripsacum, (followed by repeated hybridization with Euchlaena) it is not surprising to find in them a blending of the sharp proterandry of the one with the pronounced proterogyny of the other to produce types in which both proterandry and proterogyny are exhibited but in which neither is so marked that self-pollination is impossible.

Another great difference between Andean and North American corn is in tillering habits. Almost all North American varieties exhibit a tendency to tillering and in some the tillering is profuse. The Andean varieties which we have grown have been noticeably lacking in tillers, and Dr. Emerson tells us that during his travels in Peru he was more impressed by the absence of tillers in the corn than by any other one characteristic. Here again is a difference which may be due to Tripsacum germplasm, for Tripsacum is a plant of profuse tillering habits.

Perhaps the frequent occurrence of staminate florets in the pistillate inflorescence in North American varieties may be the result of segregation or concentration of Tripsacum genes. We have no data on the occurrence of staminate flowers on the ears of Andean corn and a comparison of the two types in this respect would be of interest. We do know, however, that Euchlaena often bears some staminate florets in the lateral inflorescences, and that Translocation segment-B isusually associated with staminate flowers at the tips of the ears. It would not be surprising for this trait to be transmitted in various degrees to corn which had become contaminated with the genes involved.

Perhaps, too, the relatively frequent occurrence of duplicate factors in the segregation of recessive characters in North American corn is a consequence of the incorporation of Tripsacum genes. Duplicate genes have been reported for aurea seedlings, piebald seedlings, orange scutellum, xantha seedlings, white seedlings (two cases), white sheath, zigzag culms, sugary endosperm, and prematurely germinating or viviparous seeds. (Cf. Eyster 1934; Emerson, Beadle, and Frazer 1935.)

The prematurely germinating seeds are of particular interest in this connection because triplicate and quadruplicate, as well as duplicate, genes have been reported (Mangelsdorf 1930). Eyster (1931) questions whether the evidence for this is conclusive because the linkage relations of the various genes which have been postulated have not been determined. Though it is readily conceded that this additional evidence would have been desirable, we are of the opinion that the rather extensive F_3 data are quite convincing and cannot be ignored. If the occurrence of these types is admitted, they become more readily understandable with the new concept of North American corn as a carrier of Tripsacum germplasm, for in Tripsacum dormancy is extremely well controlled and sometimes difficult to break, and we should therefore expect Tripsacum to contribute genes for dormancy. The occurrence of 63:1 and 255:1 ratios in the segregation of premature germination does not mean, then, that three or four genes have mutated. It may mean merely that in each case only one gene controlling dormancy has mutated but that this recessive gene does not express itself so long as its effects are "covered" by other genes from Tripsacum. This accounts, perhaps, for the fact that all the types of premature germination in which duplicate, triplicate, and quadruplicate factors appeared to be involved occurred in crosses between stocks which themselves had never segregated for premature germination. Thus a 15:1 ratio might have occurred when a strain *ge Tr* was crossed with a strain *Ge*, the *Tr* representing not an allele of a gene for premature germination but a gene from Tripsacum which "covers" the effect of the recessive *ge* gene, from maize.

Duplicate and other multiple genes are frequently associated with polyploidy, and it has sometimes been assumed, primarily because of the existence of five chromosome species in both the Maydeae and Andropogoneae, that maize is a polyploid. Powers and Clark (1937) have recently presented some evidence which, according to their interpretation, indicates that maize originated from a 7-chromosome species, and that one chromosome set has been duplicated, another triplicated. Multiple factors might also arise, however, from the introduction of genes from another species, particularly if some of the genes are additions to, rather than substitutions for, the previous ones. We have already shown (p. 160) that a gene from Tripsacum which suppresses or covers the effect of the sugary gene of maize can be introduced into a stock that is homozygous recessive for sugary, so far as its genes from maize are concerned. Here, then, is a proved mechanism for the development of duplicate genes and we know that duplicate genes occur in North American corn. Whether we are dealing with cause and effect or a mere coincidence remains to be determined. A comparison of North American and Andean varieties with respect to the frequency of duplicate genes may throw some light on the problem.

That some of the abnormalities which appear in North American corn are due to a recombination of genes or groups of genes originally received from Tripsacum by way of Euchlaena, there can be little doubt; the influence of Tripsacum is too readily discernible. During the past season we have encountered two types of corn which resemble in certain characteristics the types which segregate from Zea x Euchlaena hybrids. These are illustrated in Fig. 93. Both types occurred in the first generation of top crosses between inbred strains and the parental open-pollinated variety which in each case was a synthetic combination of numerous inbred strains, which had been rigidly selected for trueness to type. In other words, the abnormalities appeared in crosses the parents of which did not exhibit the abnormality.

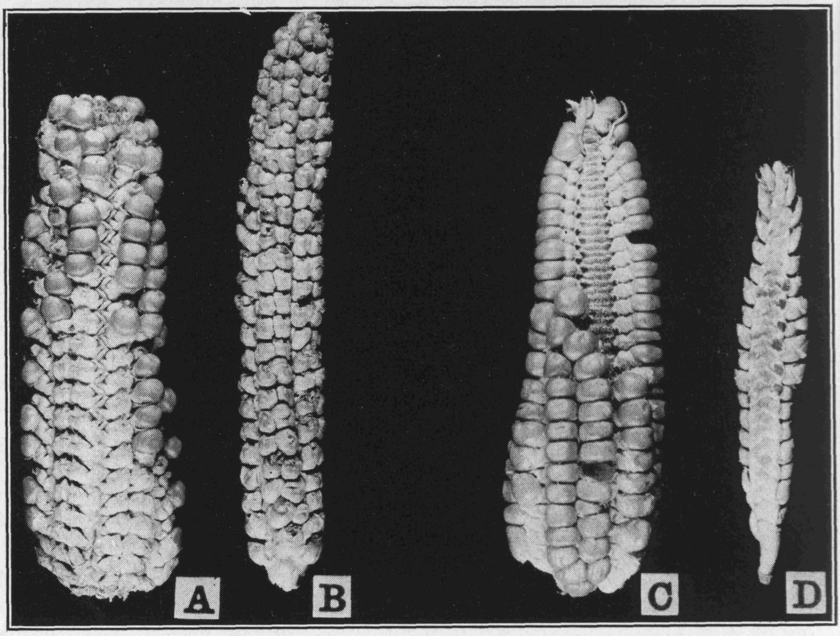

Fig. 93. Two abnormal ears of corn (A and C) which exhibit an influence from teosinte, compared with segregates from a maize-teosinte cross (B and D). Note similarity between C and D in structure and pigmentation of rachis and presence of staminate spikelets at tip.

The first type shows characteristics of Translocation segments A and C, as is readily seen by comparing it with the AC type. The resemblance includes even the cross sterility of A and C. Both of the ears illustrated were open-pollinated and were subjected to an abundance of pollen. This type appeared in two separate replications of the same top cross, so it cannot be an accident of environment.

The second type is quite similar to the 4/8 rowed corn studied by Tavčar (1935). It exhibits the staminate flowers characteristic of Translocation segment B and the brown pigmentation of the rachis characteristic of C. It is compared in the illustration with a segregate from a Zea x Euchlaena hybrid to show the similarity in structure and pigmentation of the rachis. This type appeared in all four replications of the same top-cross, a fact which indicates that it has an hereditary basis, though it occurred in neither parent. Here again there is need of genetic studies in Andean corn to determine if these and similar variations occur.

Comparative Morphology of Chromosomes

Longley's (1937) observations on the morphology of the chromosomes of Tripsacum and various forms of teosinte suggest new lines of cytological attack on the problem, for it seems very probable that the knobs found so frequently on the chromosomes of North American corn varieties came originally from Tripsacum.

We have attempted to present the average number of knobs of the various groups of maize relatives studied by Longley from the data given in his report. Since Longley's study was made primarily for the purpose of determining the comparative morphology of the chromosomes in general rather than the numbers of knobs, the character in which we are primarily interested at this point, our estimates made from his data probably contain some element of error. However, these estimates are the best available to us at the present time and we believe that they are applicable in a general way. We have done this also with the data reported by him (1938) for maize itself, and are of the opinion that the averages calculated from this paper are more accurate. In arriving at the average number of knobs listed in Longley's data, we have not considered the heavy-staining enlargement of chromosome 6 adjacent to the nucleolus to be a knob, since McClintock (1934) has satisfactorily demonstrated that it is fundamentally different. We should state also, since Longley pointed out a difficulty in distinguishing small knobs from large chromomeres in Euchlaena, that the number of knobs included in our estimates for certain teosintes may be higher than the actual numbers. This is particularly true for the teosinte from San Antonio Huixta.

Longley has shown that in Tripsacum *(T. floridanum)*, every chromosome has at least one terminal knob and several have two. He shows 22 knobs on the eighteen chromosomes of this species, all of which except one are terminal. The teosinte from San Antonio Huixta, the region where it grows as the dominant species, exhibits great variability in the knobs; but Longley illustrates, in the various series, terminal knobs at both ends of every chromosome except 9 and 10, in which knobs are shown only at one end. Our estimate, made from his data, of the average number of knobs is 17, and the total number of knob positions is 19. The teosinte from Nojoyá, a locality quite close to San Antonio Huixta, shows a total of 16 knob positions all of which are terminal. No average for this variety was computed because the data were insufficient. The teosintes from Progreso and Moyuta in southern Guatemala, which is apparently a secondary center, have a total of 11 and 14 knobs respectively with an average of 12.5 in the variety from Moyuta. All of the knobs in both of these varieties are terminal. When we consider the Mexican teosintes, however, the situation changes very strikingly. Chapingo teosinte has a maximum number of 22 knobs and an average of 17.2, not including the knobs on the abnormal chromosome 10 that was found. All of these except 5 are internal. The teosinte from Durango has a total of but 11 knob positions and an average of 9.8 knobs, of which only two are terminal. In Longley's (1938) study of chromosomes of maize from the North American Indians, the number of knobs that he reported for all varieties examined averages 4.2. The maximum number of knobs considering the various types in combination is 18, of which three are terminal and the remainder internal.

The Mexican teosintes in all of their morphological characteristics exhibit a much greater influence of maize than do the Guatemalan teosintes, and associated with this difference is a decrease in the proportion of terminal knobs. This might be explained as the result of the substitution of internal knobs of maize for the terminal knobs of the more Tripsacum-like forms of teosinte, but there is another possible explanation. Perhaps all of the knobs in all forms of teosinte as well as the knobs in the chromosomes of maize trace their origin to the hybridization with Tripsacum. If this is the case, we might well expect to find among South American varieties, particularly those of the Andean region, some which, like sorghum, have no knobs on their chromosomes.

Accordingly, a large number of varieties of South American corns were obtained through the courtesy of Dr. Merle T. Jenkins. At the date of the present publication, 83 plants representing 40 of these varieties have been studied cytologically, with special attention to number of knobs.

No attempt was made to identify the chromosomes on which knobs were found, because, as Longley (1938) has pointed out, the initial identification of the chromosomes of a variety of maize based solely on chromosome morphology introduces a considerable element of error. Certain of the chromosomes may vary in structure from one variety to the next or even within the same variety; for example, on a certain position on a given chromosome, a knob may be homozygous, heterozygous, or absent, depending upon the individual plant or variety. Also, a particular chromosome may vary in other morphological features, and even the number of chromosomes is known to vary on account of B-types. In view of these facts, a large proportion of these 40 varieties must be studied more intensively before a complete account of the status of their knobs can be given. However, a complete account is unnecessary for the present purpose, and the results of this unfinished study already are significant. The results are given in Table 40.

Table 40. *Numbers of knobs on chromosomes of maize from South America*

Variety No.	Varietal name (when known) and locality of collection	No. of knobs
119800	Buenos Aires, Argentina	2
119801	Buenos Aires, Argentina	1
119802	Buenos Aires, Argentina	3
B439	Uruguay	5
119929	Villa Rica, Paraguay	4
119930	Villa Rica, Paraguay	3
104229	Brazil	5
112743	Minas Geraes, Brazil	1
117961	Bello Horizonte, Brazil	6
117962	Bello Horizonte, Brazil	3
117963	Bello Horizonte, Brazil	6
117964	Bello Horizonte, Brazil	5
117965	Bello Horizonte, Brazil	5
117967	Bello Horizonte, Brazil	2
118000	Rio de Janeiro, Brazil	5
118505	Sao Paulo, Brazil	4
118506	Sao Paulo, Brazil	2
118779	Brazil	5
127717	Amarillo de Tucay, Urubamba, Cuzco, Peru	2
127718	Amarillo de Urquillos, Urubamba, Cuzco, Peru	0
127719	Culi de Urquillos, Urubamba, Cuzco, Peru	0
127720	Huacca-Mullu de Urquillos, Urubamba, Cuzco, Peru	0
127721	Paraccay de Urquillos, Urubamba, Cuzco, Peru	0
127722	Paraccay de Tucay, Urubamba Valley, Cuzco, Peru	0
127723	Saccsa de Tucay, Urubamba Valley, Cuzco, Peru	0
127724	Saccsa de Urquillos, Urubamba, Cuzco, Peru	0
127762	Callejon de Huaylas, Ancash, Peru	1
127763	Callejon de Huaylas, Ancash, Peru	0
127764	Callejon de Huaylas, Ancash, Peru	0
127765	Dept. of Lambayeque, Peru	0
127766	White Cuzco, Cuzco, Peru	0
127767	Maiz Amarillo, Cuzco, Peru	0
127768	Callejon de Huaylas, Ancash, Peru	0
127769	Callejon de Huaylas, Ancash, Peru	0
127770	White Cuzco Corn, Callejon de Huaylas, Ancash, Peru	0
B412	Huancayo, Junin, Peru	4
B436	Dutch Guiana	3
B437	Dutch Guiana	3
110972	Maiz Chiquito, Venezuela	4
110973	Maiz Cariaca, Venezuela	7

Although the number of plants of each variety examined was small, the number of knobs most frequently found is the number usually recorded in the table. When two or several numbers occurred with equal frequency, the whole number nearest the mean is recorded. This simplifies the interpretation of the results, although it may introduce a slight error with some varieties, on account of the small numbers of plants used. A few of the knobbed and knobless chromosome complexes are shown photographically in Figure 94.

The results shown in Table 40 are in perfect agreement with the prediction, already stated, that some of the South American varieties, particularly those of the Andean region, would be found to have entirely knobless chromosomes. The average number of knobs per variety by countries is as follows:

Argentina	2.00	Peru	0.83
Uruguay	5.00	Dutch Guiana	3.00
Paraguay	3.50	Venezuela	5.50
Brazil	4.08		

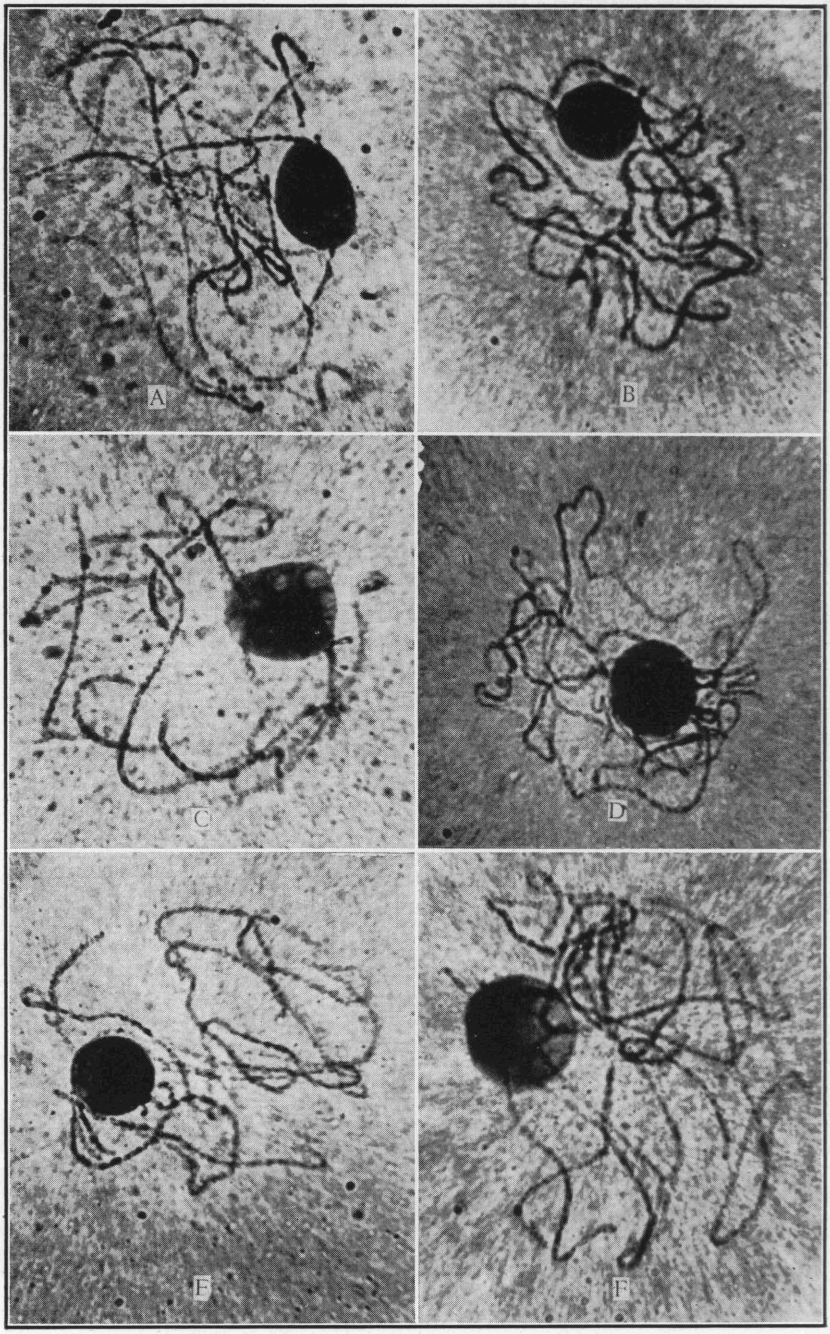

Fig. 94. Chromosome of 5 varieties of maize obtained from South America, showing numbers of knobs; X 1000. A. No. 127766, White Cuzco from Cuzco, Peru; no knob. B. No. 127720, Huacca-Mullu de Urquillos, Urubamba, Cuzco, Peru; no knob. C. No. 117965, from Bello Horizonte, Brazil; 3 knobs, greater numbers being found in other plants of this variety. D. No. 119801, from Buenos Aires, Argentina; no knob, although 1 knob was the rule in this variety. E. No. 127721, Paraccay de Urquillos, Urubamba, Cuzco, Peru; no knob. F. Same; 1 knob, found as an exception. (Black specks on the chromosomes, distinguished by clear borders, should not be confused with knobs.)

All of the knobless varieties are Peruvian, and this fact is in especially close agreement with our theory that Peru includes the primary center of domestication of maize. It seems probable that, in general, the original Andean maize has proved more profitable in Peru than the introduced varieties, and therefore, Peruvian maize is less contaminated with introduced maize from Central and North America than is the maize of other parts of South America. The knobs on the chromosomes of all of the other South American corns may be explained as coming from introduced varieties from Central and North America.

These results combined with those of Longley (1938) point definitely to some region between the United States and South America as the region where the native corns have the greatest number of knobs on their chromosomes. Longley's results show that the number of knobs on chromosomes of corn grown by the Indians of the United States increases in proportion to their proximity to Mexico, although no variety that he examined was entirely knobless. Our results show that the greatest proportion of completely knobless varieties thus far examined are original Peruvian varieties, and the greatest number of knobs occurs in Venezuela, the nearest region to Mexico from which any of our South American varieties were received. The knobs of Brazilian varieties are much more numerous than the average, while the varieties studied from other regions of South America are too few to deserve further comment.

It may be asked how the knobs of Tripsacum, which are exclusively terminal, could have assumed the internal position characteristic of most of the knobs of maize. Several ways in which this might have occurred could be suggested, and one has already been mentioned (p. 168); but there is no necessity of speculating on this problem until more is known about the nature of the knobs. In the meantime the circumstantial evidence that the knobs of maize and Euchlaena originated from hybridization with Tripsacum is quite significant. Zea, Euchlaena, and Tripsacum are the only genera of plants in which chromosomal knobs have ever been discovered. Euchlaena, which is presumably a hybrid of Zea and Tripsacum, is intermediate between the two, both in number and position of the knobs. Furthermore the most Tripsacum-like teosintes resemble Tripsacum in number and position of knobs while the most maize-like teosintes resemble maize. Particularly significant in this connection is Longley's (1938) observation that some of the varieties from the Southwest which exhibit the highest average number of chromosome knobs of any collection, also have a peculiar condition on the tenth chromosome identical with a condition found in Chapingo teosinte. Here, then, is a series of forms between maize and Tripsacum in which the number and position of the knobs is closely correlated with the resemblance of the various forms to Tripsacum. On the basis of the correlation in this series and on the basis of our tripartite hypothesis that cultivated maize had its origin in South America as a single gene mutation from a wild form of pod corn; that Euchlaena is a recent product of the natural hybridization of Zea and Tripsacum; and that new types of maize originating from this cross comprise the majority of North American varieties, we made the prediction that certain South American varieties which show no evidence of contamination with Tripsacum would exhibit knobless chromosomes. This has proved, with a few exceptions, to be the case. Since maize varieties with completely knobless chromosomes had never been previously reported, the fact that we were able to predict, successfully, not only that knobless varieties would be found, but also where they would be found, is excellent evidence that the hypothesis is a reasonably sound one, even though it is based largely on circumstantial evidence.*

When these facts are considered the evidence is quite conclusive in pointing to the development of new types of maize as the result of contamination with Euchlaena, which in turn probably received from Tripsacum the characteristics by which it differs from maize. That the infusion of Tripsacum germplasm was beneficial from the standpoint of survival of the plant under domestication is evidenced by the fact that all varieties of corn from both North or South America, except those from the Andean region, which have been examined cytologically, give indications of contamination with Tripsacum. Apparently the new types spread in both directions from their center of origin in Central America and in a relatively short time replaced the original uncontaminated corn in all regions except the Andean, where maize had been domesticated for so long a period, and had become so well adapted to the peculiar conditions there, that even the improvement brought about by the addition of Tripsacum germplasm was not sufficient to bring about a replacement of the old types by the new.

This conception of North American corn as a mixture of genes from Zea and Tripsacum, a mixture in which the proportions vary with each variety, if not with almost every plant, should, in the end, permit a more intelligent approach to the problems of corn improvement. It is quite likely that many of the problems of resistance to cold, drought, smut and other diseases will resolve themselves into terms of Tripsacum genes. The fact that many of the better inbred strains which have been isolated in the Corn-Belt in recent years exhibit the long, slender, cylindrical ears associated with a concentration of Tripsacum genes, suggests that an in-

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*It should be pointed out that any other plausible hypothesis explaining the knob positions on the chromosomes of North American maize presents similar or even greater difficulties. Some type of hybrid origin of North American maize may be considered as a basic requirement for any explanation of the positions of its knobs because the assumption of one original maize parent having the diversity of knob positions known in North American maize seems unworthy of consideration. Only one alternative hypothesis, therefore, remains: that some or all of the knob positions of maize chromosomes were obtained from teosinte, but that tesinte did not obtain them from Tripsacum. On the basis of the work of Longley (1937), we consider it a safe assumption that the forms of teosinte showing the least signs of hybridization with maize have mostly terminal chromosome knobs. Therefore, if North American maize received its knobs from teosinte, a rearrangement of the knobs is still a requirement, whether teosinte received them from Tripsacum or not. Our hypothsis has the advantage of explaining the similarity of the knob positions in teosinte and Tripsacum. The fact that perennial teosinte is almost knobless (Longley 1937) may be regarded as a discrepancy in our interpretation. However the fact that perennial teosinte is apparently an autotetraploid of comparatively recent origin, and that it is more maize-like than Florida or Durango teosintes in its ninth chromosome, suggests that it is further removed from Tripsacum in some respects than are several other varieties of teosinte, and hence might be expected to exhibit fewer knobs. Finally there is a possibility that the change from the annual diploid to the perennial tetraploid condition has had an effect upon the prominence of the knobs.

crease of Tripsacum "blood" in many of our commercial varieties may be desirable. If this proves to be the case, a very simple mechanism for introducing Tripsacum genes, or short segments of Tripsacum chromatin, into the maize germplasm can be devised. The cross of Tripsacum and maize is rather difficult to make, but if a cross of tetraploid maize and tetraploid Tripsacum is produced, it will probably result in a fertile true-breeding amphidiploid which can be fairly readily crossed with diploid corn and which can be propagated indefinitely as an easily accessible reservoir of Tripsacum germplasm.

THE ORIGIN OF TRIPSACUM

Tripsacum and Zea probably are direct descendents of a geologically remote common ancestor; the very fact that it is possible to hybridize the two genera speaks of genes which they possess in common. Even in characteristics in which they differ most strikingly, genetic studies of the segregates from hybrids indicate that each possesses genes for characters exhibited by the other. The balance between the genes with opposing forces is, however, different in the two genera.

Tripsacum, like Zea, must originally have stemmed from a perfect-flowered plant, for the morphology of the flowers in the two genera is essentially the same. Both inherited from their remote common ancestor a tendency toward monoecism resulting from the suppression of one or the other sexes in different parts of the plant. This condition had apparently proceeded further in Tripsacum than in Zea until the latter, by virtue of the mutation from *Tu* to *tu*, suddenly more than overcame the lead. Until that time, however, Tripsacum was the more highly specialized of the two.

The tendency to monoecism may, as Goebel (1910) suggests, be but the first step to dioecism, and dioecious maize has, in fact, been produced by Jones (1934) by an appropriate synthesis of mutant characters. In any case the monoecism of the two genera is of the same general type, a tendency to concentrate the staminate flowers in the terminal or uppermost inflorescence, the pistillate ones in lateral or lower inflorescences. In both genera there is a gradient from top to bottom. Thus though Tripsacum produces both staminate and pistillate flowers in all inflorescences, the terminal ones have a much higher proportion of staminate flowers than the lateral ones, and though maize usually has a complete separation of the sexes, there are numerous exceptions. Werth (1922) has presented some very interesting data which demonstrate the gradient which occurs in maize with regard to the development of staminate or pistillate flowers. In a population of 1651 plants the terminal inflorescence on the main stalk was entirely staminate on all but 29 plants. Of the 712 tillers on these plants, 377 were terminated by staminate inflorescences, 344 by mixed pistillate inflorescences. But the former were much taller than the latter. The average height for the main stalk was 171.5 centimeters; for the tillers terminating in a staminate inflorescence, 157.1 centimeters;

for those terminating in a mixed inflorescence, 112.7 centimeters; and for those bearing only pistillate flowers, 42.5 centimeters.

In this and in many other characteristics evolution in Zea and Tripsacum has proceeded along parallel, if not identical, lines, the chief differences being that Tripsacum has exhibited a tendency to polyploidy accompanied by a perennial habit of growth while Zea has apparently never varied in this direction, at least in nature. There is some evidence, too, that Zea was on the road to extinction when man appeared on the scene. It had become reduced to a single species, which was evidently becoming more and more restricted in its habitat until man rescued it from eventual extinction. Tripsacum, on the other hand, has exhibited a strong tendency toward speciation and has become more and more widespread, now occupying regions formerly covered by continental ice sheets.

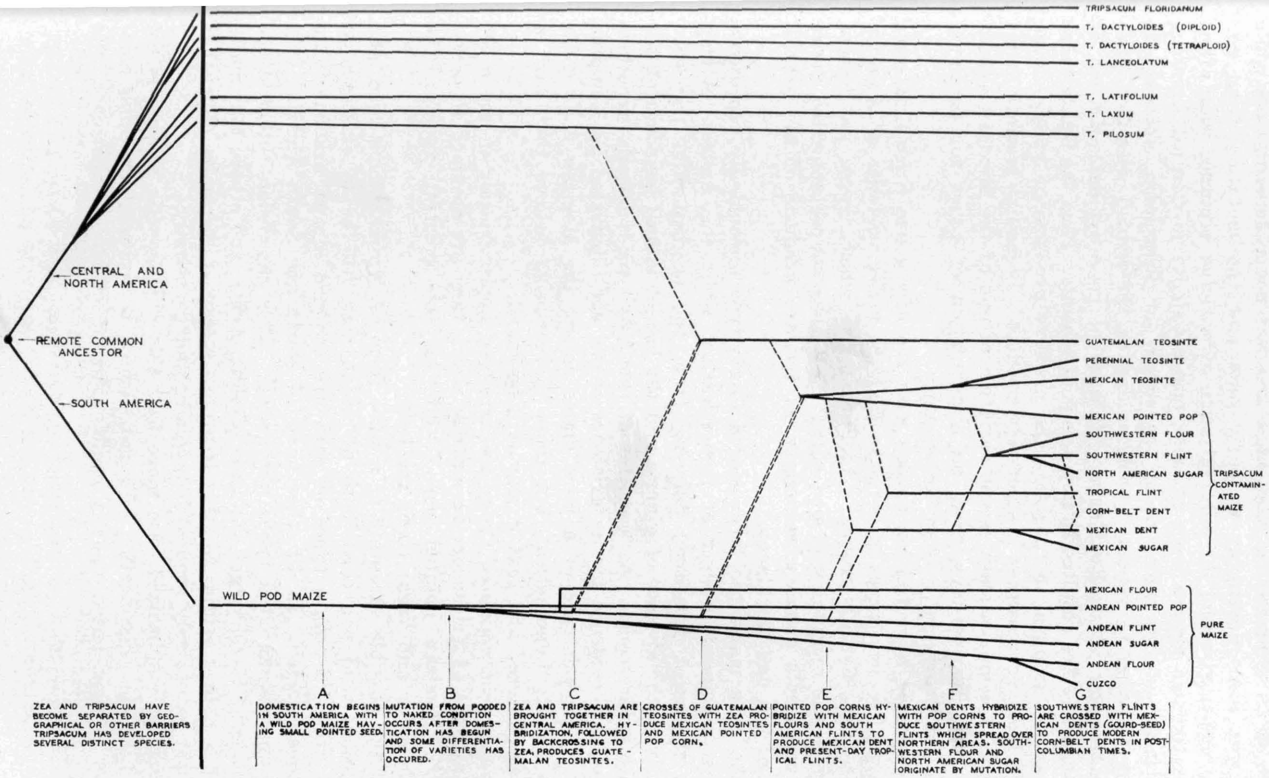
The center of dispersal for Tripsacum is probably in Mexico and Central America. There it grows in greater profusion and exhibits a greater diversity than is found elsewhere in America. From this region it has apparently spread in both directions, for Tripsacum is found in both North and South America, although it is far more abundant in the former. This may suggest that the spread southward has been more recent, and has come about through the removal of barriers which at one time separated the ranges of Tripsacum and Zea.

Until evidence to the contrary is forthcoming, we may therefore look upon Tripsacum and Zea as parallel variations descending from a remote common ancestor under very diverse environments and separated by geographical, ecological, or physiological barriers until comparatively recent times.

THEORETICAL PHYLOGENY OF THE AMERICAN MAYDEAE

Now that the evidence on the origin of Euchlaena, Zea, and Tripsacum has been presented in considerable detail, it is but another step to summarize the conclusions in the form of a hypothetical phylogenetic scheme which indicates how these three genera and their various forms have come into existence. This has been done in the diagram illustrated in Fig. 95. In considering this phylogenetic scheme the reader must keep in mind the fact that it is by no means final, and will necessarily be modified as new evidence accumulates. On the other hand, some of the conclusions are supported by good evidence, and the remainder are in accord with the available facts. The phylogenetic scheme is, therefore, nothing more than a summary of the evidence and conclusions which have already been presented in detail in previous sections.

We have assumed that the two American genera, Zea and Tripsacum, stemming from a remote common ancestor became separated in past geological periods, one confined to South America and the other to Central and North America. At the time of man's arrival in America, Zea was represented by only one species, the wild pod corn, Tripsacum by at least six species, already differentiated. Tripsacum, because of its hard bony



ZEA AND TRIPSACUM HAVE BECOME SEPARATED BY GEOGRAPHICAL OR OTHER BARRIERS TRIPSACUM HAS DEVELOPED SEVERAL DISTINCT SPECIES.

A DOMESTICATION BEGINS IN SOUTH AMERICA WITH A WILD POD MAIZE HAVING SMALL POINTED SEED.

B MUTATION FROM PODDED TO NAKED CONDITION OCCURS AFTER DOMESTICATION HAS BEGUN AND SOME DIFFERENTIATION OF VARIETIES HAS OCCURED.

C ZEA AND TRIPSACUM ARE BROUGHT TOGETHER IN CENTRAL AMERICA. HYBRIDIZATION, FOLLOWED BY BACKCROSSING TO ZEA, PRODUCES GUATEMALAN TEOSINTES.

D CROSSES OF GUATEMALAN TEOSINTES WITH ZEA PRODUCE MEXICAN TEOSINTES AND MEXICAN POINTED POP CORN.

E POINTED POP CORNS HYBRIDIZE WITH MEXICAN FLOURS AND SOUTH AMERICAN FLINTS TO PRODUCE MEXICAN DENT AND PRESENT-DAY TROPICAL FLINTS.

F MEXICAN DENTS HYBRIDIZE WITH POP CORNS TO PRODUCE SOUTHWESTERN FLINTS WHICH SPREAD OVER NORTHERN AREAS. SOUTHWESTERN FLOUR AND NORTH AMERICAN SUGAR ORIGINATE BY MUTATION.

G SOUTHWESTERN FLINTS ARE CROSSED WITH MEXICAN DENTS (GOURD-SEED) TO PRODUCE MODERN CORN-BELT DENTS IN POST-COLUMBIAN TIMES.

THEORETICAL PHYLOGENY OF MAIZE AND ITS RELATIVES

Fig. 95. Diagram illustrating the theoretical phylogeny of Zea, Tripsacum, and Euchlaena and showing how some of the present-day maize types may have come into existence.

shells, was an unpromising food plant and was never domesticated, while maize was domesticated at an early date and the mutation from pod corn to naked corn and the differentiation of varieties occurred soon after.

After the two genera were brought into proximity in Central America, hybridization of Zea with one of the species of Tripsacum, probably *T. pilosum*, followed by repeated backcrossing of the hybrid with Zea gave rise to the new genus Euchlaena. Subsequent repeated hybridization of Euchlaena and Zea resulted in new forms of teosinte. Thus the Guatemalan teosintes are assumed to represent the primary products of hybridization and the Mexican teosintes a secondary product. Perennial teosinte is regarded as a comparatively recent variation of one of the Mexican annual forms, resulting, perhaps, from an accumulation of genes for perennial growth habit, originally from Tripsacum.

The repeated hybridization of Zea with the new genus Euchlaena gave rise as well to new types of corn, so that the maize varieties of America comprise two distinct groups: 1. Pure maize which traces its descent directly to the original wild pod corn; 2. Tripsacum-contaminated maize which represents primary, secondary, or tertiary products of the hybridization of Zea and Euchlaena.

Of the pure maize the large-seeded Cuzco type undoubtedly represents the most advanced product of domestication, while the Andean pointed pop is the most primitive, differing from the original wild pod corn primarily in the absence of glumes and the loss of lateral branches of the pistillate inflorescence. As a matter of fact this type is largely hypothetical; the only evidence for its existence is one ear illustrated by Kempton (1938). The existence of a pure maize among the Mexican flour corns is also largely hypothetical, but there is reason to believe that such a type has occurred and that it may still be found.

Tripsacum-contaminated types are arranged approximately in the order of the amount of Tripsacum germplasm which they are assumed to carry, with the Mexican pointed pops exhibiting the greatest amount, the Mexican dents and sugar corns the least.

With the possible exception of a pure form of Mexican flour corn, and the original wild pod corn, both of which may still be in existence in limited areas, the pure types of corn are confined almost exclusively to the Andean region. In all other parts of North and South America only Tripsacum-contaminated types are grown. This conclusion supports the assumption of Harshberger, Kuwada, Collins, Arber, and others that maize has had a hybrid origin, for this is probably true of the maize which has been most extensively studied botanically and genetically.

It must be emphasized once more that this phylogenetic scheme is not final. Like the classification of a taxonomist, it represents nothing more than an opinion based upon a combination of evidence, experience, and observation.

Relationship of the American Maydeae to the Andropogoneae

The phylogenetic scheme presented above considers only the American Maydeae. It is becoming increasingly apparent, we believe, that the time is almost ripe for a reconsideration, and perhaps a revision, of the entire tribe. The chief criterion for membership in this tribe has been monoecism and there is some question whether too much importance has been attached to this characteristic. Weatherwax (1926), for example, regards monoecism as of minor importance, stating that it is the result of a very general tendency throughout the Gramineae toward the differential abortion of parts. Bews (1929), on the other hand, considers monoecism as a characteristic of special groups, and it is true that the monoecism which characterizes the Maydeae, both American and Oriental, is of a special type, a fact which Weatherwax failed to mention. He has, however, (Weatherwax 1926) called attention to other important differences between the American and Oriental Maydeae, particularly in the structure of the indurated shell in which the seed is enclosed. These differences, combined with a complete failure of the two groups to hybridize, suggests that their relationship is remote.

Whether or not the separation of the American and Oriental Maydeae is justified at the present time, there is at least good reason for regarding the American Maydeae as nothing more than a sub-tribe of the Andropogoneae. The suggestion is not a new one. A number of botanists including Hackel, Hooker, Bews, and Hitchcock, have at one time or another either classified the Maydeae as a sub-tribe of the Andropogoneae, or have stated that it is in reality no more than a sub-tribe. Collins (1912) pointed out that the homozygous, earless type of pod corn possessed no characteristic which would exclude it from the Andropogoneae. We have shown that this form is identical with Tripsacum in several botanical characteristics, and Weatherwax (1926) some years ago called attention to the resemblance of Tripsacum to some of the Andropogoneae, particularly Manisuris. Our own studies have shown that Tripsacum has a chromosome number which is a direct multiple of that of Manisuris.

We have every reason to believe that the common ancestor of Zea and Tripsacum was a typical Andropogonaceous plant and we suspect that this plant has given rise to several other species which have since become important crop plants, notably Sorghum (*Sorghum vulgare* Pers.) and sugar cane (*Saccharum officinarum* L.). Sorghum, like maize, is a ten-chromosome plant and the two genera have many other characteristics in common. Both are annuals with a tendency to concentrate their energy in the production of the caryopsis. There is a decided parallelism in the mutations which occur in the two genera. Some of the mutations which are common to both, such as waxy endosperm (cf. Kempton, 1921b, Karper, 1933) are of no particular significance for they are found in many distinct genera of grasses. Others, like sugary endosperm, have been encountered only in maize and sorghum. Even the unique tunicate character of maize apparently has its counterpart in the *Sorghum papyrascens* described by

Rangaswami Ayyangar and Panduranga Rao (1936). Finally, sorghum is the only genus, except Tripsacum, the pollen of which has, in our experiments, induced swelling in the nucellus of maize. Though we have never obtained hybrid seeds from these pollinations, we expect that success in this direction will come when the proper technique has been developed.

The relationship of sorghum and sugar cane is quite similar to that of Zea and Tripsacum. Hybrids of these genera have been studied by Thomas and Venkatraman (1930), Venkatraman and Thomas (1932), Singh (1934), Bourne (1935), Janaki Ammal and Singh (1936). Saccharum is, in many ways, a counterpart of Tripsacum. It is a perennial with a tendency to increase the chromosome number by irregular multiples. Like Tripsacum it devotes its energy to vegetative growth, some species producing enormous, succulent stalks. There is a possibility that Zea and Sorghum may be hybridized and that the cross of Tripsacum and Saccharum will also succeed. Attempted crosses between Sorghum and Tripsacum have always failed but the corresponding cross of Zea and Saccharum has apparently already been made. It was first reported in South America (Anon. 1934) but no real evidence was presented. More recently, however, Janaki Ammal (1938) has reported the successful hybridization of the two genera and has presented some convincing cytological evidence that true hybrids were obtained.

This cross links Zea, one of the most highly specialized of grasses, with Bambusa, generally regarded as one of the most primitive, for Venkatraman, (1937, 1938) has previously reported hybridization of Saccharum with Bambusa. Since both Zea and Bambusa can be crossed with Saccharum, they probably possess a considerable amount of germplasm in common.

As a matter of fact the entire question of the classification of the grasses is apparently due for reconsideration. Crosses of Lolium and Festuca, generally regarded as belonging to separate tribes, have occurred spontaneously and have been reproduced in the laboratory. Other wide crosses are also reported (cf. Nilsson 1930, 1933, Ulmann 1936, Allan 1937) and it is becoming increasingly apparent that in classifying the grasses too much stress has been laid on superficial morphological characteristics.

However, so far as the present discussion is concerned, we need consider only the American Maydeae, and we are convinced that both Zea and Tripsacum should be regarded as members of a sub-tribe of the Andropogoneae. Whether the Oriental Maydeae belong in this same sub-tribe, whether other genera of the Andropogoneae such as Manisuris should be included, and whether Euchlaena should be classified as a species of Zea, are all subsidiary questions which we hope to consider later.

MAIZE IN RELATION TO CULTURE AND CIVILIZATION

In one point, at least, the new evidence on the origin of maize is in much closer agreement with archaelogical and anthropological evidence than are several of the hypotheses previously proposed. It makes no demand for time beyond that which the anthropologists are willing to assign to man's period of existence in America. All of the steps involved in the evolution of our modern corn varieties—the mutation from pod corn to naked corn, the hybridization of Zea and Tripsacum to produce the new genus Euchlaena, and finally the development of new types of maize as a consequence of this hybridization—all of these changes could have occurred within a relatively short period of time.

Before considering some of the other questions involved, perhaps a brief review of the anthropological and archaeological evidence which has a bearing on the problem is in order.

Arrival of Man in America

On the question of man's origin in America there is but little controversy. Hrdlicka has shown, on the one hand, that man could not have originated in America, and on the other, that the aboriginal people of America, though divided into numerous tribes and speaking many languages and dialects, were essentially a single race of people, a race almost identical with certain Asiatic stocks. To this day the American Indian is indistinguishable from a type that still persists in Formosa, Tibet, Mongolia, and in parts of Western China, Siberia, Korea, and Japan (cf. Hrdlicka 1917).

How these Asiatic peoples may have reached the New World is another question and one which may never be completely answered, but there are three possible routes: (1) Across the Bering Strait, where only 30 miles of water separate the two continents and where on a clear day, land in one is visible from the other and where in winter a solid mass of ice sometimes connects the two shores; (2) By way of the crescent chain of Aleutian Islands to the South through which some species of plants can be traced from Japan to the Pacific coast; (3) Over actual land connections north of Bering Strait which are thought to have existed until comparatively recent times and over which many of our American species of animals, closely related to similar species in Asia, may have travelled.

With regard to the time of man's arrival on this continent there is also still some question. There was probably more than one migration, the New World being rediscovered again and again. The last wave is probably represented by the Eskimos, who, finding the territory to the South already occupied, were forced to adapt themselves to life in Arctic regions. Hrdlicka thinks that the first migration could not have occurred until Northeastern Asia was well populated and he estimates that this did not take place more than 10,000 years ago. Recent discoveries in the Southwest of peculiar spear points, known as Folsom, associated with the skeletal remains of species of bison, now extinct, have led some anthropologists to revise upward this estimate of man's period of existence in America. But until the actual remains of man are found under conditions which leave no question of their antiquity, this evidence of an earlier arrival will remain incomplete. At the most, man probably could not have been in America over 25,000 years, which is but a fraction of the time assigned to his existence in some other parts of the world.

Actually, so far as the origin of maize is concerned, it makes not the slightest difference whether man arrived here 10,000 or 25,000 years ago. In either case the time available for the domestication of maize, the development of modern types, and the spread of the plant over two continents, is more than ample.

These aboriginal Americans, transplanted Asiatics, drifted more or less at random through the New World, making their way through wildernesses where man had never passed before. We can be certain that their movements were not systematic, "not similar to those of marching armies or the migration of Israelites from Egypt to Canaan" (cf. Thomas 1907). It is more likely, as Lord Averbury (cf. ibid.) has stated, that "man originally crept over the earth's surface little by little, year by year, just, for instance, as the weeds of Europe are gradually creeping over the surface of Australia." How long this random spread may have required we have no way of determining; but it probably was no more than a fraction of man's period of occupation of America, perhaps a few centuries or a few thousand years at the most. In any case he eventually populated the land on two continents and the adjacent islands and finally succeeded, without help or inspiration from outside, in developing two great civilizations, the Andean (Inca), and the Middle American (Maya and Aztec), which in certain material and intellectual characteristics were equal to any of the civilizations of the Old World. Both of these civilizations were based upon the culture of maize, and indeed maize is the only American crop plant which could have served in this capacity.

Ancient Cultures and Civilizations

The Andean Civilization

Most distant from man's point of entry into the New World is the Inca civilization of the Andes, which during its period of greatest expansion included parts of Peru, Bolivia, Ecuador, Colombia, and Chile. This civilization had its beginnings, according to Means' (1936) interpretation, about 1100 A. D.; but it was preceded by three highly developed cultures, the Chimu and Nasca of the coast and the Tiuahuanaco in the highlands. All of these cultures probably had their origin before the time of Christ, but how long before, there is no way of determining from the data at hand. Systematic archaeological studies of Andean remains have not been as extensive as in some other regions and conditions have not been particularly favorable for the preservation of some types of remains. The sequence of cultures in the Andes has been extremely difficult to determine because there are few instances where entire villages have been engulfed by sand or other deposits; stupendous landslides have in some places swept away in a few hours the accumulation of centuries; and finally, the Spanish conquerors, in their greed for treasure, destroyed some of the most important evidence (cf. Bingham 1917).

The evidence that still remains, however, proves that in the arts, the crafts, engineering, government, and agriculture, the Andean people made greater advances than did any other ancient American people.

The Chimu pottery of the coast in its grace and beauty, simplicity and sincerity, is inferior only to some of the best of the Grecian work.* Some of the Peruvian textiles woven from the native cotton and the wool of the vicuña are of such a fine weave that they are not ordinarily duplicated by the modern machinery of today (cf. Means). The masonry walls of the Incas are the most intricate that have ever been built in any part of the world. Using stone tools and transporting huge stones weighing as much as 361 tons (cf. Squier 1877), without machinery or power except that supplied by human labor, the Incas constructed magnificent walls and buildings in which the stones were fitted together, without mortar or other binding material, with such nicety that in many places a knife blade cannot be inserted in the crevices.

Feats of engineering include accurate topographical surveys, clay models of cities in which every building is shown to scale, an elaborate system of aqueducts for irrigation, a network of paved highways touching every part of the Empire and traversing mountain passes at altitudes of more than 13,000 feet, and crossing torrential streams with suspension bridges.

There were skillful surgeons among the ancient Peruvians, for many of the skulls found in the prehistoric graves show evidence of successful trepanning; of 400 crania with artificial openings which Tello (1913) examined, 250 showed evidence of healing, indicating that the patient had survived—*an astonishing percentage of success for such a delicate and difficult operation.*

The government of the Incas was one of the most sensible and successful which has ever been developed. Paternalistic, but practical in its paternalism, it required that every inhabitant do his share and in return it guaranteed him a share in the necessities of life while permitting him wide latitude in the affairs of the family, the community, and the practice of his religion. When disaster befell one region of the Empire, assistance was immediately forthcoming from other regions. The ever-normal granary was an accomplished fact in Peru, centuries before it received serious consideration by the "advanced" American civilization of today.

But it is in agriculture perhaps more than in any other activity, that the Andean people made greater advancement than have any other American people. Not only did they domesticate more species of edible plants, but they were also more successful in the domestication of

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*Cf. Baessler (1902-1903) and Lehman and Doering (1929) for illustrations.

animals. Their cultural methods were far superior to those of other ancient American civilizations. Every square foot of tillable soil was utilized and in addition agriculture was pushed far up the steep slopes by the use of masonry terraces (cf. Cook 1916). Fish and guano were used as fertilizer (cf. Joyce 1912), and water was supplied in many places by an elaborate system of irrigation which tapped the streams sometimes far above the agricultural lands, and carried the water by aqueducts to the higher terraces from which it was led by successive steps to the lower fields. The Andean region is the only place in America where agriculture generally had passed beyond the exploitative stage and where the soils were systematically built up rather than carelessly depleted of their fertility.

Of all the plants which were cultivated for crop purposes, maize was by far the most important. It was grown at altitudes ranging from slightly above sea level in the coastal valleys to more than 12,000 feet on the islands of Lake Titicaca. Except at the higher altitudes where it is replaced by the potato and quinoa, it was and still is, the staple crop. It may, in ancient times, have been important even at the higher altitudes. Squier states that maize was being grown on the island of Lake Titicaca when he explored that region, although it could not be grown on the mainland because of the slightly lower temperature. Bandelier (1910) later reported that maize was grown around Lake Titicaca on the northern exposures but not on the southern. A very slight change in mean temperature occurring over a long period of years may have changed a region which was once marginal for corn production to a region which is now submarginal. Furthermore, as Cook (1925) has pointed out, it was at one time possible to grow corn profitably in regions where it cannot be so grown today because the Incas had constructed huge granaries with capacities for storing several years' supply of grain, so that the frequent crop failures which occur in a marginal region were not so disastrous as they would be today when these storage facilities have been abandoned.

Many types of corn were in use, as is amply demonstrated by representation on the vases and figurines and by actual ears recovered from prehistoric graves. But all of these which we have seen, either as representations or as remains, are of the Andean type, whose characteristics have already been described. Nowhere are found the North American pointed pop corns or the long, slender, cylindrical, straight-rowed types common in North America.

If the numerous representations of maize in the ceramics of Peru are not sufficient testimony to the importance of this plant in Peruvian life, the stories of the early explorers and missionaries leave no doubt about the place of maize in the economy and religious and social life of the people. Not only was maize the staff of life, but it was also the foundation of the national drink *chicha*, which was made usually by the old men and women who chewed the grains and after mixing them well with saliva deposited the masticated material into brackish water where fermentation took place in about eight days. A particularly potent drink, *vinapu* was made by first allowing the maize to soak and sprout in water, after which it was mashed and allowed to ferment in the same water. Another drink, noted for its ripeness and potency, was the special maize beer prepared by the young men during the months of puberty ceremonials (cf. Means 1936).

Almost every month of the Peruvian calendar included some ceremonial in which maize played a part. Before the great Feast of the Sun, a special bread or pudding known as *canca* was prepared by the chosen women; and during the feast it was partaken of with great solemnity (cf. Means).

In the month of sowing, great quantities of maize beer were sprinkled in the fields; and after planting, a sacrifice of llama, guinea pigs, maize, and other products was offered. To make good fortune doubly certain, the priests during the period from planting to sprouting of the maize, refrained from eating anything except toasted maize kernels and herbs without salt (cf. Means).

In the fourth month there occurred a very important festival during which a special maize-gruel, known as *sancu,* was made, and while still hot was used by all householders to anoint their faces, thresholds, and niches where food was kept. All the fountains of the city were likewise anointed with the gruel, and the faces of the mummies as well. These rites were followed by a great feast, which was terminated with prodigious drinking of the maize beer (cf. Means).

Another ceremony, a rather gruesome one, occurred during the festival —30 white llamas brought from all points of the Empire were sacrificed. The blood of the animals was mixed with maize to produce a blood pudding which was then divided into many tiny loaves. These heaped upon large golden platters were carried throughout the throng by the chosen women of the Sun, every person taking one loaf for himself and one for any sick relatives at home. Loaves of this sacred bread were also sent by fast messengers to every village of the Empire (cf. Means).

The last month of the year, about May 22 to June 22, was devoted to the celebration of the harvest. During this month all families observed the rites of *Mama Sara,* the Mother maize, by burying a small amount of maize, wrapped in the richest cloth which they possessed, in a little hole on the farm (cf. Means). The Mama Sara or spiritual essence of maize was also represented by a figure covered with ears of maize or a vase fashioned as an ear (cf. Markham 1910).

The Incas, the rulers of the Empire, recognized the importance of maize and of agriculture, and to evince their respect for the art lying at the foundation of their state, and to elevate and dignify labor, they established a custom of imitating at the terraces at Cuzco, the planting and harvesting operations. With pomp and ceremony the Inca himself went to the terraces and with a golden pickaxe commenced to break up the soil. When the crops of maize had ripened, he again went out and harvested the first ears. These crops grown and gathered under the direct ministrations of the Son of the Sun were regarded as sacred and, like the seeds from the sacred Island of Titicaca, were distributed to be sown on land dedicated to the Sun throughout the Empire (cf. Squier).

The story of the sacred corn from the Island of Titicaca is of particular interest. Here at an altitude of 12,600 feet in a region not adapted to corn at the present time, the Incas had built elaborate masonry terraces which were filled with soil brought from a distance. On this artificial farm land was grown the sacred maize which was distributed to the temples and convents of the Empire, one year to one, one year to another, so that each received some of the seed at intervals. This was in turn grown in the gardens of the temples and the crop distributed among the people of the various provinces. Some grains were scattered among the stores in public granaries to preserve this supply from corruption. So strong were the superstitions surrounding this sacred grain that it was believed that the possession of a single grain of this maize would protect a person against lack of bread during his lifetime (cf. Squier).

The Middle American Civilization

The Middle American civilization includes both the Maya and Aztec, but since the latter is largely an offshoot of the former, it will suffice for our purpose to confine this discussion to the Maya.

Despite the fact that the remains of the Maya civilization have been studied more intensively and systematically than those of perhaps any other American culture, and despite the fact that the Maya had perfected a calendar and a means of writing and had left a written chronology, there are very few data to tell where, when, and how the Maya civilization had its origin. Various writers have had the Mayas originating in Egypt, Carthage, Java, Southern India, or the lost continent of Atlantis, and one writer has even had them descending from the Lost Tribes of Israel. Modern authorities, however, are agreed that the Maya civilization is an indigenous one, developed by the American Indian, without assistance from any other race. Nevertheless, its beginnings are hidden in remote antiquity. It appears to have blossomed forth, almost full blown, in a region which today is considered extremely unpromising as a site for a civilization.

Spinden (1917) is of the opinion that the Maya civilization developed only after the widespread distribution of the archaic culture, remains of which are found in Mexico, Guatemala, Salvador, and Honduras, all within a general area inhabited by tribes of Nahua-speaking people whom he considers to have been the originators and spreaders of agriculture. This widespread archaic culture which presumably preceded the Maya seems, however, to have had very little if any influence upon the latter, while on the other hand, as Morley (1920) points out, the Nahua culture has been decidedly influenced by the Maya. Morley suggests that the Maya may have originated as a branch of the Huasteca, a Maya-speaking people living on the Gulf Coastal Plains of Mexico between Tuxpan and the Panuca River, the separation having occurred before the Mayas had developed the characteristic features of their civilization. Lothrop (1933) has recently shown that the culture which preceded that of the Maya is a blend of traits borrowed from the early valley of Mexico, from South America, and from a yet unidentified local culture.

But whatever the beginnings of the Maya civilization, it eventually reached, in certain respects, a pinnacle higher than that attained by any other American people. Situated in Honduras, Guatemala, and Yucatan in a region that today is mainly tropical forest, the Mayas developed an empire that at one time comprised more than twenty large cities with magnificent buildings and monuments.

Though the masonry of the Mayas was not equal to that of the Incas, though their textiles were greatly inferior to those of Peru and their ceramics not to be compared with the pottery of the Chimus, and though their dwellings were crude and their agriculture primitive, still the Mayas were unique in their intellectual achievements. They were the only American people to perfect the calendar, a calendar which excelled by far the chronology of the ancient Egyptians. The Maya calendar is exact to the day within a period of 374,000 years, which is as accurate as our own Gregorian calendar (cf. Morley 1936); and the Mayas were so well versed in their study of the astronomical phenomena upon which the calendar is based that they were able to predict far in advance the eclipses of the sun. The Mayas were unique in developing the essential elements of our modern arithmetic, including numeration by position and a symbol to represent zero, all of which they accomplished at least 2,000 years ago, five centuries before the Hindus had developed their Arabic notation (cf. Morley 1936). Finally, they were unique in originating the art of writing, which Huntington (1917) calls one of the few supremely great human achievements.

Three manuscrips and numerous monuments inscribed with hieroglyphics, the interpretation of which has been made possible by the discovery in 1863 of a manuscript history of Yucatan, composed during the first century after the Spanish conquest, tell us something of the events which occurred and the time at which they took place.

The interpretation of the hieroglyphics shows how many *cycles* of 144,000 days each, how many *hatuns* of 7,200 days each, how many *tuns* of 360 days each and how many *uinals* of 20 days each had elapsed since the beginning of the chronology at a hypothetical point corresponding approximately to the year 3400 B. C. or the year 3140 B. C., depending upon which correlation is used. There is no question of the accuracy of the calendar, but there has been some controversy among archaeologists in correlating the Maya calendar with Christian chronology.

The Maya civilization had two great periods—the first or Old Empire confined largely to Guatemala and Honduras, which began before the time of Christ and ended about the year 600 A. D. (Spinden Correlation); and the New Empire confined largely to Yucatan, which had its beginnings shortly before the collapse of the Old Empire, reached its peak in the tenth to twelfth centuries, and was already in a serious state of decline when the Spaniards arrived on the scene.

The collapse of the Old Empire is as mysterious as its beginnings. Huntington (1917) has attributed it to a change in climate and has attempted to show that a correlation occurs between the ebb and flow of Maya civilization and the growth of tree rings in the giant redwoods of California where he assumes that the climatic changes were negatively correlated with those in Central America. Spinden suggests that the decadence in art which characterizes certain periods of Maya history may have been accompanied by a corresponding decadence in the physical, moral, and political condition of the people. Cook (1909) was of the opinion that the gradual intrusion of perennial grasses, with which the agriculturists were unable to cope because they lacked domestic work stock, finally resulted in making the land unfit for agriculture. Morley (1936) has reached the conclusion that the downfall of the Old Empire was the result of the old economic law of diminishing returns. Due to the depletion of the land it became necessary to go farther and farther afield to raise the corn to support the populations in the cities, until a point was finally reached when the culture of maize was no longer profitable. Still other writers have suggested other explanations, including wars, earthquakes, disease epidemics, insect plagues, or religious superstitions.

The Mayas like the Incas were dependent upon agriculture for existence. Among the crops grown were maize, beans, squashes, gourds, peppers, tobacco, cotton, mandioc, sweet potatoes, peanuts, and cacao. Maize was the staple food and even today constitutes 75 to 85 per cent of the diet of the Maya Indians (Morley 1936). The Maya methods of agriculture, ancient as well as modern, were quite primitive as compared to those of the Peruvians. The methods in use today are as follows: As soon as the rainy season is over, usually in January or February, a new piece of forest is cleared. The fallen trees are allowed to dry during March and sometimes part of April, after which they are burned. After the first rains, which appear usually in early May, the corn is planted among the charred trees by the use of a pointed, fire-hardened stick.

Corn is not usually put into successive cultivation for more than one season, as the yield usually diminishes very appreciably in the second and third year. After lying fallow for two to five years, a field may be returned to cultivation again.

The importance of maize in the economy of the Mayas is attested by the prominence which it played in their religion. Representations of the maize god are numerous and the famous "foliated cross" at Palenque is, according to Joyce (1914), a conventionalized maize plant. Accurate representations of actual ears are, however, rare; and we have encountered only one, the small clay figurine illustrated by Maler and now in possession of the Peabody Museum of Harvard University.

The Mayas like the Peruvians practiced divinations with maize grains and like the Peruvians sent the dead upon their journey with a supply of maize, sometimes even filling the mouth of the corpse with maize meal.

The myths and legends of the Mayas regarding maize are too numerous to review in detail. The most interesting one, perhaps, is that which has man created from the meal of maize. Another relates that certain gods or god-like men, recently arrived in the land, were much displeased with living conditions and planned to reclaim the natives from barbarism. Accordingly four chiefs were sent to a distant land to get new ideas. They returned bringing with them "ears of yellow maize and white." The newly found maize rounded out their scheme of existence and became their chief reliance for food (cf. McNair 1930).

Other American Cultures

The Andean and Middle American civilizations are the oldest in America and all other advanced cultures trace their origin at least in part to these two. It is unnecessary in this monograph to deal with the numerous North American cultures which were flourishing when America was discovered, for only Central America-Mexico, and the Andean region can be seriously considered as centers of the primary domestication of maize. Suffice it to say that there was nowhere an advanced culture of which maize was not the foundation. Maize, beans, and squashes; these three crops furnished the basis of all aboriginal agriculture; and, of the three, maize was unquestionably the most important.

Maize, Agriculture, and the Archaic Culture

Preceding all of the advanced cultures of the New World was a more primitive stage of culture known to anthropologists as the "archaic." When, where, and how this archaic culture had its beginnings in America are questions which have given rise to considerable controversy, but which still remain, at least in part, unanswered.

Writers of a previous generation seemed to have but little doubt that the oldest cultures were to be found in the Andean region of South America. Some of the later authorities, however, have inclined to a Mexican or Central American origin of the archaic culture. Spinden (1917), for example, suggests that agriculture and the archaic culture originated in the highlands of Mexico and were spread from there by Nahua-speaking peoples. And the fact that the earliest cultures discovered in Peru are already well advanced, leads Means (1936) to conclude that culture had been introduced there from elsewhere, probably from Central America, before 600 B. C. More recently, evidence is accumulating to show again that the archaic culture probably had its beginning in South America. The invention of agriculture and the domestication of maize both have important bearings on this problem.

There can be but little doubt that agriculture was the basis of practically all cultural advancement in America. All authorities who have studied this phase of the problem seem to be in complete agreement on this point. Payne (1892), for example, thinks that the principal features which distinguish civilization from savagery are traceable mainly to the substitution of an artificial for a natural basis of existence. Spinden (1917) states that "Agriculture may be named as the antedecent for all the high cultures in the New World." The close agreement between the maps which Spinden presents showing the distribution of pottery and of agriculture in America almost proves his point.

That maize was the basic crop in all American agriculture there also can be no doubt. It was one of the chief crops grown wherever agriculture was practiced in all parts of America;* and as Nuttall (1926) has stated, "The history of the development of maize is inseparable from the history of the origin and development of civilization on the American continent."

This is not surprising, for all the great civilizations of all time have been based upon the culture of cereals; and some authorities consider it an axiom that no advanced civilization can develop without cereal culture. No one, perhaps, has expressed this conviction more clearly than Payne. "So far as concerns the New World," he states, "the above facts tend to support the general proposition, to which the history of the Old World suggests no exception, that nothing worthy the name of civilization has ever been founded on any other agricultural basis than the cereals." And again, "Cereal agriculture, alone among the forms of food production, taxes, recompenses and stimulates labour and ingenuity in an equal degree."

It is significant that maize is the only cereal in the world which could have served as the basis for a highly developed agriculture in America. And here again we cannot refrain from quoting Payne, who has anticipated many of our own conclusions by almost fifty years, and has stated them with a facility which we find it difficult to match. On the importance of maize to the American agricultural complex, he states:

"Whether, if the wild form of maize had not existed, cereal agriculture would have had any place whatever in aboriginal American advancement is extremely doubtful. The smaller cereals cannot be profitably grown without some means of reducing the entire surface of the seed-plot to a state of tilth; a process which involves great labour, and can only be pursued on an adequate scale by the aid of the plough and of the large labouring animals. A narrow wooden or bronze spade was the most advanced agricultural implement of the New World: and, in the absence of the ox and the horse, the tillage of the soil had to be universally accomplished by the unassisted labour of man. In such circumstances, the wide prevalence of maize-agriculture suggests that this cereal must be especially suitable for cultivation by slightly advanced populations; a suggestion which is at once confirmed by an examination of its nature. The chief characteristics of maize, when compared with other cereals, is the extraordinary size both of the plant and of its grain. The principal varieties range from six to twelve feet in height; in some fertile soils it

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*Cf. Wissler (1916) for an interesting discussion of maize as a typical culture complex.

reaches a height of sixteen or eighteen feet. Each plant produces from two to five ears; the ear varying from six to ten inches long, contains from twelve to sixteen rows of closely set grains; and the grain is larger than that of any other cereal known. This gigantic size directly facilitates its cultivation by limiting the number of plants that can come to maturity in a given space; while smaller cereals require the laborious tillage of the entire surface of the field, maize can be successfully cultivated without this process, and by means of the fire-hardened stake alone. All that is necessary is to burn the trees and wild plants on the surface of the plot, to make holes at proper distances, to drop in the seed, to stir the earth around the young plant, and to keep it clear of weeds, and in from two to four months' time, according to the quality of the soil and the degrees of rain and sunshine, the seed yields from one to four hundredfold. Two crops can be grown in a year on the same plot; and in some places three and even four successive crops are taken. While the ease with which this unrivalled corn is produced placed cereal agriculture within the reach of man at a comparatively early stage of advancement, the large returns which it yielded greatly stimulated its cultivation; and at the time of the Discovery it had already spread over most of tropical and temperate America, where no animal capable of agricultural labour existed, and in many parts of which the idea of reducing the soil to tilth was wholly unknown. Thus did nature to some extent compensate America for the want of the great domestic animals by endowing it with an unique cereal, the largest and most productive known, and capable of being profitably cultivated without them."

The Origin of American Agriculture

When we recognize the importance of maize to the agriculture of the New World it might seem, at first glance, that it is necessary only to determine the center of origin of maize in order to determine simultaneously the center of origin of agriculture and the archaic culture. This was apparently the reasoning followed by Spinden (1917) when he assumed that agriculture in America had only one point of origin because maize, beans, and squashes were common products wherever agriculture was practiced, and who concluded that the archaic culture had its origin in Mexico, presumably because teosinte, the closest relative of maize, was common there, and at that time unknown elsewhere.

If we could accept Spinden's premise, the problem would be a relatively simple one, for if the evidence on the South American origin of maize is as conclusive as we believe it to be, we should need to look no further for the origin of agriculture and the archaic culture. Unfortunately the situation is not so simple as Spinden supposed, for though he is quite correct in his statement that corn, beans, and squashes were common products in all agricultural regions; and though the corn in all parts of America comprises but a single species, this is not true of the beans and squashes and of several other crop plants, as a comparison of the agriculture of the Andean region and the Central American-Mexican region will show.

A study of the origin of American agriculture, therefore, must consider more than maize; even more than maize, beans, and squashes combined. It must examine all of the main crops which constitute the agricultural complex, the cultural methods, the evidence from domestic animals, the conditions under which agriculture was practiced, and the stage of advancement which it reached.

On one more point practically all authorities are in agreement—that American agriculture is an American invention, and that it developed independently of the agriculture of the Old World. It is exceedingly doubtful that the early migrants from northeastern Asia knew anything of agriculture at the time of their departure; but if they did, it was certainly forgotten long before they reached a place in America where it could be practiced.

There are only two general regions in America where agriculture became so highly developed that it supported elaborate civilizations—the Andean region of South America and the Mexican-Central American region. We shall first compare the agriculture in these two regions and later consider the possibility of an independent origin of agriculture in still other areas.

Evidence from Domestic Animals: The dog is the only domestic animal common to the two regions. The Peruvians had at least three distinct kinds; the Mexicans several types, one of which was reared and fattened as a meat animal. But the dog is a poor measure of man's success in the domestication of animals, for it instinctively joins man on his hunts, and so practically domesticates itself. In any case, the dog was almost as widely distributed in America as man, and probably accompanied him on his long trek from Asia.

All other domestic animals of the New World are strictly of American origin. The animals of the Old World—the horse, ass, ox, sheep, goat, camel, and chicken—were completely absent. The lack of draft animals had a decided effect upon the type of agriculture which developed and the absence of dairy animals and egg-producing poultry undoubtedly affected the nutritional standards of the aborigines.

With the possible exception of the turkey*, the only truly domesticated animals of the New World were the guinea pig, the llama, and the alpaca, all of the Andean region. The guinea pig was raised for food almost throughout the region. The llama and alpaca, both distant relatives of the Old World camel, were reared only at high altitudes, the llama as a beast of burden and a source of meat, the alpaca primarily for its wool.

Means (1918) questions whether the llama is more than a partially domesticated animal, for it feeds itself, does without shelter, and prefers

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*There is some question whether turkeys should be regarded as highly domesticated, for after 400 additional years of domestication they are still semi-wild, and there are no essential differences between the wild and domestic flocks.

to breed away from human surroundings. All of these remarks might be made of cattle on the range in the Southwest and all are commentaries on the environment in which the animals are reared, rather than upon the degree of domestication. There is some question, too, whether Means' observations are completely accurate, for Payne refers to an illustration by Wiener of a terra-cotta vessel showing a small two-storied structure in which llamas were housed in the lower story. This would indicate that shelter was sometimes provided. Payne also mentions the fact that the llama pastures are sometimes irrigated, a fact which is evidence that the animals are not independent of man's ministrations for their food supply. Finally, the llama is physically quite different from its wild relative the guanaco, and several writers, notably Markham, have called attention to the diversity of coat colors in the domesticated llama as compared with the single coat color of the wild guanaco . The alpaca has become so completely domesticated that it is dependent upon man for survival, and its wild prototype is no longer in existence (cf. Markham 1910), unless it be assumed, as Reinhard (1912) has done, that the alpaca is a hybrid of the wild guanaco and the wild vicuña. In either case, a long period of domestication is indicated.

Neither the llama nor the alpaca, however, has been domesticated to the point where lactating females can be milked (cf. Hahn 1905) ; and to this extent they are not so completely domesticated as the herbivorous animals of the Old World, almost all of which, under the proper circumstances, will give down their milk to the herdsman.

In comparison with the use of the llama and alpaca by the South Americans, the Mayas and Mexicans have even less to their credit. They possessed only two partially domesticated animals, the turkey and the bee. The latter has been largely replaced by another species introduced from Europe, and the former is still almost as much at home in the wild as under domestication.

Ducks, geese, partridges, and pheasants are also mentioned as domestic animals of the Mexicans and Mayas. Ducks and geese were also known in Peru. There is no real evidence that they were truly domesticated in either region, and certainly it is very doubtful whether pheasants or partridges could be considered domesticated. In fact, the only animals that can claim this distinction are the guinea pig, the llama, and the alpaca, all of the Andean region.

Perhaps the Andean people met with animals which were more amenable to domestication than those encountered in Mexico or Central America; but perhaps the difference is one of time rather than raw material.

Evidence from Cultural Methods: In cultural methods the Andean tribes were far in advance of any other American people. Skill in agriculture is acquired only by gradual steps, covering a long period of time. Unlike a calendar, or a means of writing, which may be the product of one or a few brilliant minds, or a superior social system which may be the handiwork of an outstanding dynasty, proficiency in agriculture comes only as the result of the accumulated experience, through the generations, of masses of people. Given time enough, agriculture usually passes through three periods—a period of "exploitation" during which the virgin soil is literally mined of its fertility, a period of "conservation" during which efforts are made to stem the growing losses of fertility from cropping and erosion, and a period of "reconstruction" during which the soil may actually be built up and improved. In the United States, we are only now beginning to enter the second stage. Europe has entered the third only within the past few centuries; and crop yields in certain regions of Europe are now higher than they were when America was discovered. But the ancient Peruvians were practicing an advanced type of agriculture long before the Conquest. Their terrace agriculture was so old that at the time of the arrival of the first Europeans they knew nothing of its origin, ascribed it to the gods, and considered it to be coeval with the world itself (cf. Payne).*

In contrast to this the Mayas, for the most part, practiced the primitive *milpa* type of agriculture, preparing their fields by burning the vegetation and moving to new fields each year or two. When this practice reached a point of diminishing returns, they abandoned their magnificent cities and moved to new lands (cf. Morley 1920).

It does not follow, however, that the Maya agriculture was young merely because it was primitive. No people have ever passed beyond the exploitative stage of agriculture voluntarily; they have always been forced into making the change.

The type of agriculture practiced by the Mayas is characteristic of forested regions in all parts of the world, and is more a measure of environment than of age. Furthermore, recent evidence (Lundell 1933) indicates that the Mayas, in some of their mountain valleys, did build terraces after extensive cultivation had resulted in serious erosion and silting of the lowland lakes. And it is known that the Mexicans had learned to practice irrigation in the arid regions.

The evidence from cultural methods, therefore, tells us only that the agriculture of the Andean region was very old; it does not prove, although it suggests, that the agriculture of Mexico and Central America was younger because it was, on the average, more primitive.

Evidence from Domesticated Plants: Perhaps the most conclusive evidence on the origin of American agriculture should be sought in the cultivated plants. The American crop plants, for the most part, are distinct from those of the Old World and all were confined to America in pre-Columbian times, with the possible exception of the sweet potato, which may have reached the Polynesian Islands not long before Magellan's arrival (Merrill 1937). Only the bottle gourd, *Lagenaria vulgaris* Ser., a species capable of spread by ocean currents, was common to both the Old World and the New, and here the evidence of an Old World origin, based upon a diversity of types, is quite conclusive (Vavilov

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*Cf. Cook (1916) for a good description of Peruvian terrace agriculture.

1931). All other American crops of any importance with the exception of the sunflower, *Helianthus annuus* L., and the Jerusalem artichoke, *Helianthus tuberosus* L., originated either in South America or in the Central American-Mexican region. The problem is to determine which region is the primary and which the secondary center of domestication.

The South American region must in turn be subdivided into two distinct regions—the tropical lowlands and the Andean highlands. Only in the latter, however, did civilization accompanied by a highly developed agriculture come into fruition. It seems logical, therefore, to compare first the cultivated plants of the two American centers of civilization, considering later the effect which the agriculture of the South American lowlands may have had upon these two, each of which has had its proponents as the primary center of domestication.

Cook (1925) has made an extensive study of Peruvian crops with particular reference to those which are still known by names derived from the Quichua language and hence were presumably in use before the Conquest. He lists some 70 species in this category, about half of which he considers to be endemic to Peru. Vavilov (1931a) has criticized Cook's list for inexactness because in some instances a clear distinction between genera and species has not been made and because the bottle gourd, *Lagenaria*, which is of Old World origin, has been included. His criticism with reference to the gourd is certainly not pertinent, for this plant was indeed among those grown in Peru before the conquest, the only claim that Cook has made for it. In spite of this, and other criticism, Cook's list has remained a very useful one, and its accuracy in many instances is attested by plant remains found in prehistoric Peruvian graves (Safford 1917b).

Cook did not commit himself, except by implication, to a Peruvian center of origin for the cultivated crop plants of America; but he did point out that if the crops which were common to the two regions, Peru and Central America, were omitted from consideration, Peru still had a long list of important food plants at its disposal, while Central America and Mexico had only one or two.

Vavilov (1931a), after a consideration of the extensive data of Kuleshov, Bukasov, and other Russian investigators, concluded that the Central American-Mexican region is the primary center of domestication of the American crop plants, Peru a secondary center. As evidence for this conclusion he presents a list of 66 species which he believes to be of Central American-Mexican origin, including in this list maize, beans, and several species of squashes. Of the 66 species in this list 16 are not food plants but ornamentals; and a large number of the remainder are not truly domesticated plants, being used more frequently in the wild state than under cultivation.

A consideration of the evidence available from the studies of Safford (1917a, b), Popenoe (1919), Cook (1925), Kuleshov (1929, 1930, 1933), Bukasov (1930), Zhiteneva (1930), Standley (1930, 1937), Vavilov (1931a), Erwin (1931, 1936a, b), Lundell (1933), Parodi (1935), and

Vestal (1938) leads us to the conclusion that neither Peru nor Central America-Mexico can be designated as the one primary center of domestication, but that domestication proceeded more or less independently in the two regions, the indigenous crops in each being supplemented by other crops introduced from the South American lowlands.

Of the numerous crops grown in the two regions, the following important ones are known, with a reasonable degree of certainty, to have been common to both:*

1. Maize
2. Beans
3. Squashes
4. Mandioc or Cassava†
5. Sweet potatoes
6. Cotton
7. Tobacco
8. Peppers
9. Tomatoes
10. Peanuts
11. Amaranthus
12. Gourds

The gourd may be omitted from further consideration because it is an Old World plant. Of the remaining eleven genera at least five—cotton, squashes, beans, tomatoes, and amaranthus—are represented in the two regions by distinct species or sub-species.

The squashes of the Andean and Central American-Mexican regions are quite distinct. The chief species of the former region, *Cucurbita maxima* Duch., is completely unknown in the latter (Erwin 1936a, Bukasov 1930, Zhitaneva 1930), while *C. mixta* Pangalo of Mexico is not known in Peru. Even one of the species which the two regions have in common, *C. moschata* Duch., is represented by distinct types, a brown-seeded one in South America, a white-seeded one in Mexico; and the two are sufficiently different to be regarded as distinct sub-species (Bukasov 1930).

The beans of the two regions present a similar situation. *Phaseolus acutifolius* Gray, the tepary bean of Mexico, is not known in Peru. The Mexican lima bean is a distinct form designated as *microsperma*. *Phaseolus vulgaris* L. and *P. multiflorus* Willd. are common to both regions, but though Mexico and Guatemala exhibit 246 forms of *vulgaris*, compared to 77 in Peru, the yellow wax types are completely absent in the former region and the collections from the two regions represent distinct groups (Bukasov 1930).

The tomato of Peru is the large-fruited *Lycopersicum esculentum* Mill. The tomatoes of Mexico and Central America are the small-fruited cherry tomato, *L. esculentum* var. *cerasiforme* Alef., and the currant tomato, *L. pimpinellifolium* Mill. The latter is also known in the Andean region but *L. esculentum* is the chief domesticated form.

Even the amaranthus in the two regions appear to be distinct, that of Mexico being designated as *A. paniculatus* L., that of Peru as *A. caudatus* L. (Safford 1917a).

The cottons of the two regions afford perhaps the most clear-cut

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*There are many other plants common to both regions. This list includes only the more important cultivated crop plants.

†The roots of this plant are used in the manufacture of tapioca.

evidence of distinct types. The Peruvian cotton, *Gossypium peruvianum* Cav., is closely related to and is considered a sub-species of the Sea Island cottons, *G. barbadense* L., which furnish the basis of the long staple cotton culture in Egypt and the irrigated valleys of Arizona and California. The Mexican cotton is *G. hirsutum* L., the short staple cotton of the United States cotton belt. All are 26-chromosome cottons and hybridization is easily effected, but there is usually some sterility in later generations of the hybrids between the *barbadense* and *hirsutum* groups.

The six remaining crops common to the two regions are apparently represented by the same species in both. These are maize, *Zea mays* L.; sweet potatoes, *Ipomoea batatas* Lam.; peppers, *Capsicum annuum* L.; peanuts, *Arachis hypogaea* L.; mandioc, *Manihot utillissima* Pohl.; and tobacco, *Nicotiana tabacum* L. It is a significant fact that all of these, with the possible exception of maize, are unquestionably of South American origin. Even Vavilov, who argues for a primary center of domestication in Central America and Mexico, concedes a South American origin for all of these plants except maize, though in the case of peppers he postulates an independent center in Central America.

It is very significant, too, that all of these plants, with the possible exception of tobacco, are lowland plants, or at any rate extra-Peruvian plants. Peppers and peanuts are undoubtedly of Brazilian origin. Maize probably had its wild habitat in the River Plate basin and may have extended into Brazil. Mandioc and sweet potatoes are unquestionably plants of the tropical lowlands, and the number of wild species of Manihot which are found in Brazil would indicate that this crop had its origin there. Even tobacco is thought by some authorities to be of lowland origin, though related species of *Nicotiana* are widely distributed in the highlands.

All of these considerations force us to the conclusion that both the Andean region and the Central American-Mexico region drew upon the South American lowlands for a number of their important crops, supplementing these with indigenous species which were domesticated independently in the two regions. In no other way can we account satisfactorily for the fact that some crop plants are essentially the same in the two regions, while others are quite distinct. An alternative assumption, of course, is that all of these crops originated in South America and that agriculture has been practiced so long in both regions that the Andean forms and Central American-Mexican forms have in some cases become differentiated to a point where they are now considered as distinct species or sub-species. This hypothesis might be tenable were it not for the fact that in some genera, indigenous wild species occur in both regions, and the still more important fact that there is no evidence of an intercourse between the Andean and Central American-Mexican regions so far as crop plants are concerned.

We must admit that these conclusions are quite different from those which we anticipated. When we first suspected that teosinte is a recent development having no part in the origin of corn, we concluded almost immediately that corn had its origin in the Andean region, and that a movement of corn and other crops from Peru to Central America and Mexico could be demonstrated. Later when it appeared evident that corn, though it had its primary center of domestication in the Andean region, probably originated as a wild plant in the lowlands, we were still of the opinion that a migration of the agricultural complex from the Andean region to the Mexican-Central American region could be shown, because so many of the important crops of the latter were clearly of South American origin. But we have been compelled to abandon these preconceived ideas and have been forced to the conclusion that there is, at present, no tangible evidence of a direct interchange of crops between Peru and Central America and Mexico.

There are too many useful plants in each region which have never found their way to the other. Take for example, cacao, *Theobroma cacao* L. This was one of the most important plants in Mexico and Guatemala. Cocoa beans served as money and a good slave could be purchased with 100 seeds. Taxes or tribute were paid with it, and it furnished the basis for the chocolatl which was so lavishly consumed by the wealthy Aztecs (cf. Hall 1914). Montezuma is said to have consumed 50 cups of this beverage daily, and accounts of the expenditures of the Royal Palace of Mexico included 100,000 tons of cocoa and 200,000 tons of maize in a single year (cf. Whymper 1921). This may be a Spanish exaggeration, but the ratio between tons of cocoa and tons of maize is an interesting commentary on the importance of cocoa. Cocoa was so important to the Mayas that they had a special god *Ekchuah* who had charge of the cacao plantations (cf. Standley 1930), and Linnaeus in giving the plant its name recognized its importance and value for his botanical name for cacao, Theobroma, means "food of the gods."

In spite of the great importance of cocoa in Central America and Mexico, and although wild species of Theobroma occur in Brazil (cf. Correa 1909), there is no evidence that it was known in the Andean region before the Conquest. Safford (1917b) noted that cacao was not included in the plant remains from prehistoric Peruvian graves, and Cook (1925) found no Quichua word for it in the vocabulary of the present-day Peruvians. Yet the cocoa bean, which contains between 40 and 50 per cent of fat, is one of the most nutritious and concentrated of the American food plants. Perhaps the great superority of cocoa to the stupefying Peruvian narcotic, coca (*Erythroxylon coca* Lam.), in its mildly stimulating properties, and its nutritive value, may account in part, at least, for the superior intellectual achievements of the Mayas as compared with those of the Peruvians.

But for all its valuable qualities, cocoa appears to have been completely unknown to Peru before the Conquest, though it is grown there now, and would certainly have been eagerly adopted by the ancient Peruvians had they known of it. We can only conclude that it was never brought to their attention.

On the other hand, the Peruvians had a number of crops which the inhabitants of Mexico and Central America would undoubtedly have welcomed had they known of them. Among these are quinoa, *Chenopodium quinoa* Willd.; the potato, *Solanum tuberosum* L.; and numerous tuberous rooted crops including *Oxalis tuberosa* Mol., *Tropaeolum tuberosum* Ruiz and Pav., *Canna edulis* Ker., *Ullucus tuberosus* Caldas, and others of minor importance.

Particularly significant is the absence of the cultivated potato in Mexico and Central America in pre-Columbian times. Cortez did not see it, Hernandez (1651) did not mention it, and the evidence now available indicates that it did not reach North America until Irish immigrants introduced it into New Hampshire in 1719 (cf. Safford 1925). Yet the North American Indians adopted the new crop very eagerly. Will and Hyde (1917) state that the potato became very popular with the Mandans after it was introduced to them in 1832. We can be certain that the Mexicans would have grown this crop had they known it, for they were accustomed to digging the small wild potatoes which grew in the highlands.

It might be argued that potatoes and other numerous tuberous rooted crops of the Andean region failed to find their way into Central America and Mexico because they are propagated by perishable tubers which would not have survived long periods of transportation. This argument might be more easily entertained were it not for quinoa, one of the most important of the highland crops in Peru, which was also completely lacking in Mexico and Central America, although its seeds could easily have been transported.

The apparent lack of direct interchange of important crop plants between these two regions suggests to us that agriculture developed more or less independently in these two centers of civilization. Both have drawn upon the contiguous South American lowlands for several of their most important crops including maize, sweet potatoes, mandioc, peppers, peanuts, and perhaps tobacco. But aside from these lowland crops, there was an independent process of domestication in the two regions, and the fact that a number of additional crops were common to both indicates only that several indigenous genera were common to both and in some cases the same genera were amenable to domestication in both regions. This is not at all surprising, for the environmental conditions of the Andean region can be duplicated in parts of Central America and Mexico; and the Indians, who never allowed the food possibilities of any plant to escape their attention (cf. Yanovski 1936), would have domesticated a number of the same genera in each region, arriving at the end, however, with somewhat different types in the two regions. Had Tripsacum been more promising as a food plant, we can be reasonably certain that there would have been two Maydeaceous cereals in America instead of only one.

It is not at all unusual for agriculture to be partly or even wholly based upon the culture of plants which are not indigenous to the region. Merrill (1933) has pointed out that neither Mesopotamia nor Egypt was the home of the plants upon which their agriculture was based, but both regions were contiguous to points of origin of important food plants and borrowed their agricultural crops from these neighboring lands. Nor is the conception of an independent origin of agriculture in two distinct regions of America contrary to experiences in other parts of the world.

The relation between the human race and agriculture has been suprisingly uniform in all parts of the world. Agriculture, like many other inventions, has usually been the child of necessity; primitive people have never invented it until they were compelled to do so. They have, in fact, shunned agriculture when it was already invented for them, if they could eke out an existence without it. The abundance of wild acorns in California, of wakas in southern Oregon, of wappato along the Columbia, of camas and kous in Idaho, and of wild rice in the lake region of Minnesota and Southern Canada have all, according to Spinden (1917), been effectual barriers against the invention and spread of agriculture among the tribes inhabiting these regions. An abundance of game may be an equally effective deterrent. Harshberger (1893) states that the Kiowas, living in a region where bison were abundant, considered agriculture a degradation. Primitive people will even abandon agriculture after they have learned it if they can secure a food supply by other means. Witness the decay of agriculture among the Cheyenne and Arapahoes of South Dakota when they acquired horses and were able to chase the buffalo (cf. Will and Hyde 1917).

But if all this is true, it is equally true that primitive people will invent and practice agriculture whenever the necessity arises and when the proper conditions for agriculture are at hand. Thus agriculture has had an independent origin in various parts of the world and, what is more, has followed parallel or identical paths of development in corresponding regions. In forested regions in all parts of the world primitive peoples have practiced a crude type of agriculture similar to the milpa agriculture of the Maya. In arid regions where water was available from streams, peoples in all parts of the world have invented and practiced irrigation. And in steep mountainous regions terrace-agriculture has been invented again and again. In these and many other respects the human race has resembled some of the species of social insects; it has always responded in the same way to certain stimuli. What, therefore, is more natural than that agriculture should be invented in America whenever and wherever conditions were favorable for such a development?*

Primitive Agriculture in South American Lowlands

We have spoken thus far of a possible independent development of agriculture in the Andean region and in the Mexican-Central American region. We must now draw a distinction between the highly developed agriculture which furnishes the foundation for advanced cultures and

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*Since this was written our attention has been called to a very valuable paper by Sauer (1936) in which the factors involved in the origin of American agriculture are discussed at length. Several of our conclusions, arrived at independently, are in agreement with those of Sauer who concluded that: "The single origin of American agriculture . . . would appear to be a far more difficult thesis to vindicate than that of a plural origin . . ."

civilizations, and the migratory agriculture practiced by semi-nomadic hunting tribes. The former can develop only in regions whose climate and geographical features combine to stimulate agricultural progress; the latter may be initiated in any region where the population tends to outrun the supply of game, and where easily propagated food plants are available. But even with this distinction in mind we can discern only one additional region in the Western Hemisphere where agriculture may have had an independent origin, the lowlands of South America. Through all of North America, north of Mexico there were no plants except the sunflower and Jerusalem artichoke which were promising material for domestication, and no matter how favorable otherwise the conditions for stimulating agriculture may be, the raw material for domestication must be at hand.

Spinden (1917) is of the opinion that agriculture would be more likely to originate ". . . under conditions that were hard rather than under those which were easy. Under an environment producing a healthy but hungry population, particularly a semi-arid environment, which would offer special inducements to agriculturists. Here they would encounter no heavy work in preparing the soil and irrigation would make them masters of nature."

Somewhat at variance with the views of Spinden, the views are those of Vavilov's (1931a) who is of the opinion that the most ancient agricultures are those of Abyssinia, China, India, and the Mediterranean, all of which developed in non-irrigated regions.

Payne (1892) suggests that agriculture probably originates first with root crop culture. He states:

"It scarcely admits of doubt, though the materials for verifying the conclusion are but scanty, that in general the cultivation of food-roots has preceded and served as an introduction to that of cereals. The number of species the roots of which can be employed as food, the wide extent of their distribution, and the higher alimentary value and greater importance of roots as food-resources in the savage life, when compared with the seeds of cereal grasses in their rudimentary or natural stage, all indicate roots as the earliest objects of tillage; and these indications are confirmed by the circumstance that while wild culmiferous grasses prefer marshy situations, the principal cultivated food-roots appear to be for the most part natives of some comparatively dry and friable soil. As the mere disturbance of light soil in the search for roots has in itself the character of tillage, their artificial production may be said to be suggested by the process of collecting them in the wild state. The gathering of wild grass-seeds, usually effected by beating or shaking the ripened grain into a basket, while the plant remains rooted in the marshy soil, gives no hint of the method of their artificial production. The act of planting a root, on the contrary, as has been well observed, scarcely differs from that of digging one up; and the familiar 'woman stick' of digger tribes, a simple pointed and fire-hardened stake, is also the general implement of primitive agriculture. So easy is the transition that the manioc, the most valuable among the roots, is even yet in rich soils cultivated by merely dropping a piece of the stalk into the hole from which the mature root has been extracted; one digging operation thus suffices for gathering the old crop and planting a new one. In the case of many of the alimentary roots, a single tuber where several are produced by one plant, or a fragment of the old one where only one exists, suffices to ensure a renewal of the supply, although the degeneration of successive crops in consequence of exhaustion of the soil speedily suggests the transfer of the process of reproduction to virgin earth; a change most directly indicated in the case of perennial plants such as the Brazilian arrow-root, which continues to produce fresh tubers, though of diminishing value, during several years, and the sweet potato. In the case of the last named root, which in virtue of its productiveness and wide distribution, takes the second rank among the tropical food-roots of the New World, the method of reproduction is suggested by nature with remarkable clearness. At the joints of the numerous trailing stalks which it sends forth in all directions, fresh roots are produced by simple contact with the soil, forty or fifty new centres of growth being often produced from a single plant. Even if the plant is left on the ground when the root has been taken, new tubers grow from its joints after the first shower of rain; and the method of laying down the shoots, by which one plant is usually cultivated, thus appears to be an imitation of nature of the simplest kind. When it is added that roots require little or no attention between the planting and digging of the crop, it is obvious that their cultivation is perfectly consistent with the wandering habits of savage life; and the manioc and other roots are still in fact largely cultivated by tribes in Guiana and Brazil, who remain substantially in the savage state. After digging and consuming the crop and making provision for a new one, they quit the district for several months, seeking other supplies, and do not return to the clearing until the new supply of roots is ready for use."

A consideration of Payne's arguments, together with a knowledge of widespread culture of mandioc by primitive tribes, leads to the suggestion that agriculture may have had its first point of origin in the lowlands of South America where the wild species of Manihot are common. Later, the other lowland food plants, first sweet potatoes and then maize, were brought into the complex. Perhaps a root-crop agriculture was developing at the same time in the Andean highlands where the potato, tuberous Oxalis, and other tuberous-rooted plants were indigenous. In any case, once the planting of food plants in the lowlands was learned, the advantages of the alluvial fans in the river valleys would have commanded attention, for these provided a combination of fertile soils and freedom from competing forest vegetable which could not have long been overlooked. And when agriculture began to be practiced in the river valleys of the eastern slopes of the Andes, it was on the way to a sustained and rapid development and to an eventual spread throughout the Andean region, for the river valleys are so many natural avenues of approach from the lowlands to the highlands.

The eastern slopes of the Andes comprise literally hundreds of narrow precipitous valleys where man once entered would find his movements decidedly restricted, and the game supply limited, but where the practice of agriculture would yield an abundant and stable food supply. The climate, as many writers have pointed out, is almost ideal for the development of an advanced culture or civilization; not so hot as to be enervating, nor so cold as to tax all of man's resources in the mere task of keeping alive. As agriculture proceeded farther and farther up the valleys, terracing and irrigation became necessary, and thus we find in this region the greatest development of agriculture which has occurred anywhere in the New World.

Geographical Features in Relation to Domestication

Of even more importance, perhaps, is the fact that the Andean region, as no other in America, provides the ideal conditions for the rapid development of many distinct varieties of crop plants. The natural division of any species into numerous sub-groups, isolated from each other by geographical barriers, is usually conducive to the development of distinct varieties even without selection. It is no more than a matter of separating the original germinal diversity into various fractions, and in "emancipating" mutant genes which would be functionless in larger populations. If any of the food-plants of the Peruvians were indigenous in the mountain valleys, there were undoubtedly already many distinct varieties before man appeared on the scene. After his arrival the evolution of new types would have proceeded even more rapidly, for as Wright (1931) has concluded from his studies of evolution in Mendelian populations:

"The only practical method of bringing about a rapid and non-self-terminating advance seems to be through sub-division of the population into isolated and hence differentiating small groups, among which selection may be practiced, but not to the extent of reduction to only one or two types. The crossing of the superior types followed by another period of isolation, then by further crossing and so on *ad infinitum* presents a system by means of which an evolutionary advance through the field of possible combinations of the genes present in the original stock, and arising by occasional mutation, should be relatively rapid and practically unlimited."

These conditions which Wright sets up as necessary for a rapid advance are met in the Andean region as they are nowhere else in America, although they exist to a lesser extinct in Mexico and Central America. The isolation is insured by the geography of the region. Some of the isolated groups were probably already in existence when primitive man reached Peru. Man provided a means of bringing the groups together, which in some species at least probably resulted in opportunities for hybridization. Yet movement from one valley to another was so restricted that hybridization in many cases was probably followed by another period of isolation. These processes were accompanied by constant selection, first natural and later artificial, so that all the conditions necessary for a rapid development were present.

Seen from this viewpoint, there is no necessity of crediting the Indian with remarkable skill in plant breeding as some writers have done (cf. Kempton 1936). Though he did, indeed, succeed in domesticating nearly all of the American crop plants which are grown today, and though his successors have added but few new species to his list of domesticated plants, or made notable progress in improving those which they appropriated, there is no evidence that the Indian was a plant breeder in the sense that he shaped his material to fit a pre-conceived ideal. His role, at least in the earlier stages, was an unconscious one. He provided the opportunity for occasional hybridization to occur and his ministrations permitted certain types to survive which might have been lost in nature. In the later stages he probably practiced selection to the extent of propagating from specimens that were obviously superior for his needs. Except for this he was no more than an innocent bystander, and the great diversity of types which he left as a legacy to the white man is not so much a measure of the skill which he displayed as it is of the environment in which he operated and the time which must have been available for this natural mechanism to function.

The Andean region and the highlands of Central America and Mexico, however, are the only two regions in America where there has existed this extremely favorable combination of conditions for the domestication of plants and the development of an advanced agriculture. The lowlands of South America possessed a number of promising food plants, but the necessary geographical features were lacking. The mountainous regions of North America exhibited the desired geographical features but short-lived, easily-propagated food plants for domestication were absent. Which of these two first-named regions first began to practice agriculture, it is impossible to determine; but the evidence from domesticated animals and plants and from cultural methods would indicate a greater age for the agriculture of the Andean region. In any case, so far as the Andean region is concerned, it seems evident that a highly advanced agriculture, and hence a highly advanced culture, must have occurred first in the valleys of the eastern slopes rather than in those of the western slopes as some recent writers have assumed. The agriculture of the inter-Andean plateau may be older than either one; at any rate it is probably older than that of the valleys of the western slopes.

Possibility of an Early Indigenous Agriculture in Middle America

The agriculture of Central America and Mexico may have had its origin entirely from the migratory, lowland agriculture of South America. There is no doubt that a number of important crop plants were introduced from this region, and these may later have been supplemented by indigenous species which were domesticated, once the fundamentals of agriculture had been learned. On the other hand, it is quite possible that a type of agriculture with beans, squashes, and cacao, as a basis was already being practiced before the South American crops were introduced. The fact that the Nahua word for the peanut is a derivative of the word for cacao (cf. Standley 1930) would indicate that the South American peanut was introduced only after cacao was well known.

If agriculture was already known in Central America at a very early date, the introduction of three such valuable crops as maize, mandioc, and sweet potatoes to a people already partially skilled in the art of agriculture would have produced effects nothing short of revolutionary.

History shows that there is a universal tendency for populations to increase more rapidly than the food supply. The inexorable Malthusian Law may, in the case of primitive people, be temporarily thwarted by the invention of agriculture. Although the practice of agriculture permits a much greater population to exist in a given area than does a hunting and fishing life, proficiency in agriculture is acquired but slowly while the population dependent upon it begins to increase rapidly, so that the net gain in release from the struggle for existence is relatively slight and the growth of cultures and civilizations is ordinarily a slow and cumulative process depending more, perhaps, upon the settled existence and the stability of the food supply than upon the actual abundance of food. Occasionally, however, to a people already practicing agriculture, new inventions, new discoveries, or the exploitation of other peoples brings about an increase in the food supply far in excess of the needs of the population. Under these conditions leisure becomes available and man, temporarily released from the daily struggle to feed himself, devotes his energies to many new activities including arts, crafts, and sciences, sometimes making phenomenal progress in a short time.

The Andean civilization and the Maya civilization of Central America may represent examples of these two phenomena. The Andean civilization has every appearance of a culture which has developed gradually over a long period of time as the people became more and more proficient in the art of agriculture and more and more successful in the domestication of plants and animals. The Maya has all of the characteristics of a civilization which blossomed quickly as the results of a sudden increase in the food supply leading to phenomenal progress in certain intellectual and material activities, while others, especially those in which participation is general, and in which proficiency usually comes slowly as the result of the accumulated experiences of generations, lagged far behind.

If there are such differences between the Andean and Central American civilizations, to what may they be attributed? Perhaps maize was one of the factors involved. It is not inconceivable that the early people of Central America and Mexico, finding their population outstripping the supply of game, which was not too abundant at best, had invented and developed the agricultural technique to a point where they could sustain themselves with such crops as they had been able to domesticate from the indigenous species at hand; cacao, beans, squashes, amaranthus, and others. Their culture developed slowly, not because of a deficiency of land but for a lack of satisfactory crop plants. Into this complex may have come quite suddenly the extremely productive food plants from the lowlands of South America—maize, mandioc, and sweet potatoes—which yield more food for a given amount of labor than any other American plants, and more than almost any of the Old World plants. Under these conditions the food supply would have increased much more rapidly than the population. Leisure would have become available to an extent that it had never been before, and to a people already entered into the first stages of culture, and already leading a settled existence, the release from the constant struggle to feed themselves must have given a tremendous impetus to the pursuit of the arts, the crafts, and the sciences.

Such a situation has its counterpart in the extremely rapid growth of our modern American civilization, which is also largely the result of providing skillful and experienced agriculturists with new crops and new opportunities, and which, like the Maya civilization, has made phenomenal progress in some activities while lagging far behind the older civilizations in others.

The Spread of Maize and Agriculture

Weatherwax (1936) contends that there is no sound basis for attempting to trace the origin and migration of corn by arranging agricultural varieties from different localities in an evolutionary series. This is, in the main, true. Yet the situation is not completely hopeless, for if the evidence on the origin of corn, previously presented, be accepted, we can devise a crude sort of evolutionary series. In the section on the origin of corn, we have already suggested how the principal types of corn known today may have come into existence. Furthermore, although new types of corn are constantly arising through hybridization and selection, there is in many varieties a high degree of stability in certain characteristics which persists with little change through long periods. Many of the modern varieties of the Andean region, for example, find exact counterparts in prehistoric replicas; and much of the corn of Europe is, according to Kuleshov (1930), essentially the same as the corn of Cuba, even after four and a half centuries of separation.

But even with such partially established facts at our command, the data must be interpreted with considerable caution and many more data must be assembled before a final picture can be drawn. Also it is impossible to study the spread of maize without examining at the same time the entire agricultural complex, for the data at best are still so meager that it is necessary to focus all available evidence on the problem in order to approach a solution. Recognizing all of these circumstances we may examine the evidence.

It is reasonably clear, we believe, that the Andean region received maize, sweet potatoes, mandioc, and several other crops from the South American lowlands. After these plants, particularly maize, had been improved by domestication in the Andean region, some of the varieties were disseminated over the lowlands, spreading more or less centrifugally over all of South America and finally reaching Central America and Mexico. Only the late-maturing, hard-seeded, tropical flints were capable of passing through the equatorial zones, however, so that there would have been but little diversity in Mexico and Central America for many centuries, had not hybridization with Tripsacum, and subsequent crossing with the new genus, Euchlaena, brought new types into existence in a relatively short time. These new types, being hardier and better suited to culture by primitive tribes than the original South American corn, spread in both directions from Mexico and Central America. Again, however, the tropical regons of Central and South America served as an effective barrier against the spread of flour and dent types so that only the hard-seeded types such as the tropical flints and pop corns were widely disseminated south of Mexico. At the present time the most common varieties in tropical South America are the small-seeded flints and pops which show evidence of Tripsacum infection in the knobs on the chromosomes and in other characteristics.

The corn of the West Indies is of the same general type as that of Central America. The orange yellow endosperm found so frequently in Panama is also common in Cuba. Yet there is little evidence of a direct spread of agriculture from Central America to the West Indies; for cacao, one of the most important plants in the former, was absent in the latter before the Discovery, although it was quickly adopted in the West Indies when introduced there by the Spaniards, and its culture soon became an important enterprise. It seems likely, therefore, that the corn now grown in the West Indies, though tracing back originally to Central American types, was introduced from South America.

A migration of agriculture from the West Indies to Florida would logically be suspected. It is only a short distance from Cuba to Florida and anthropologists have evidence of migrations into Florida from the South, an earlier Arawak movement which extended well into the State and a later Carib movement which touched only the Southern tip of Florida. Harshberger (1893) states that the Florida Indians had a South American word for corn, and he was of the opinion that corn had entered the United States by two routes, one through Florida, the other through Mexico. Collins (1919b) has questioned this conclusion, partly because there is so little resemblance between the corn of the eastern United States and that of the West Indies and partly because corn becomes progressively less important as we pass down the Mississippi and around the Gulf to Florida.

There are some varieties of the West Indian type grown in the southern states, particularly along the Gulf Coast, but perhaps these are recent introductions. On the whole, the present-day varieties of the entire Cotton-Belt show a much greater resemblance to Mexican corn than to West Indian corn. The latter is predominantly flint corn, while the 77 corn varieties collected by Kuleshov (1929) in southern United States comprised

81.8 per cent of dent varieties, almost the same percentage, 80.6, which he found in northern Mexico. Whether the distribution of the corn of today has a resemblance to the pre-historic distribution is a moot question. It is certain, however, that the dent corns were known in the southern states in very early times; for as already mentioned, Gilmore (1931) found dent corn among the plant remains of the Ozark cave-dwellers, and Beverly described dent corn in Virginia at an early date (cf. Carrier 1923). Furthermore, the Mexican corns are predominately white, three-fourths of all dent corns being white, according to Kuleshov (1930); and the southern United States has long been noted for its preponderance of white corn. In fact, white corn has predominated in the South for so long that there has been, until the discovery that yellow corn is richer in vitamin A (or its precursors) than white (cf. Steenbock and Boutwell 1920), a decided prejudice in the South against any but white corn. As a matter of fact we should, on *a priori* grounds, probably expect the corn of the southern United States to be of Mexican origin, for Mexico is the center of diversity of the dent corns; and these, being adapted to the southern United States, would certainly have been preferred to the West Indian flints for human consumption. Thus, though flint corns were probably introduced into the southern United States from both Mexico and the West Indies, the dent corns eventually became predominant.

Against the theory of a marked West Indian influence upon the agriculture of the southern United States is also the fact that there has been no real evidence that mandioc, which in the West Indies was almost as important as corn, if not more so, was ever introduced into the United States. True, Hariot in 1585 (cf. Carrier 1923) described a root crop grown by the Indians as far north as Roanoke Island, which some authorities have taken to be mandioc. Carrier, however, thinks that this plant was wampee rather than mandioc. Erwin (1936b) finds that the squashes grown by the Seminole Indians are identical with the "Cushaw" and "Sweet cheese" varieties known to the seed trade, both of which resemble the white-seeded *C. moschata* of Mexico.

On the whole, there appears to be more evidence against a West Indian introduction of maize and agriculture into the southeastern United States than there is in favor of such a view, or at any rate it is obvious that whatever influence the West Indian introduction may have had is secondary to the Mexican influence, and has been overshadowed by it.

The agriculture of the Pueblo region of the Southwest, comprising parts of Colorado, New Mexico, Arizona and Utah, is undoubtedly also of Mexican origin. Though anthropologists have found but little evidence of a cultural effect of one region upon the other, the evidence from crop plants is indisputable. The Pueblo region had only one important crop plant, the sunflower, which is not of Mexican origin. The Pueblo squash is the white-seeded Mexican *Cucurbita moschata;* the beans are similar to Mexican beans. The present-day cotton, *Gossypium hopi,* which according to Jones (1936) is identical in fiber characteristics with the cotton used in weaving the ancient textiles, is in reality no more than a variety or subspecies of the Mexican *G. hirsutum*. It hybridizes readily with the latter, and the hybrids are completely fertile. There are no differences between the two which might not have come about as the result of generations of culture in differing environments. The evidence, furthermore, indicates a movement from Mexico to the Southwest rather than the reverse, for neither cotton nor beans are indigenous to the Pueblo region, while the sunflower, which is indigenous to the United States, was not grown in Mexico. Even today it is found only in the extreme northern part and there it is known as *Maiz de Tejas* (Bukesov 1930), which indicates that it was introduced from elsewhere, and after corn was already known.

That the corn of the Pueblo region shows an interesting evolutionary trend has already been mentioned (see p. 256). The earliest culture in this region, designated as Basket-Maker I, is not associated with crop plants. Remains of pine-nuts and other natural foods are found, but no maize. Basket-Maker II is associated with a flint corn, the typical tropical flint of Central America, with its large cobs, small seeds, and irregularities in the rows of grain. In the next stage known as Pueblo I the Mexican dent types appear. Not until the stage known as Pueblo II is reached at about 900 A. D. do the long, slender, straight-rowed typical North American types appear. These are apparently an indigenous development for they are not known in Mexico.

The agriculture of the northern United States shows a decided influence of the Pueblo region. The crops for the most part are the same and the corn varieties are similar to the long, slender, straight-rowed flint and flour corns which grow in the Pueblo region today.

Even the Mound-Builders, who presumably represent one of the earlier cultures, apparently possessed this type, for Wittmack (1880) states that the corn unearthed from the Ohio mounds is usually slender, eight-rowed, with the rows sometimes distinctly separated in pairs.

The similarity of the Northern and Southwestern varieties is evident not only in the ears but also in the plants, which tiller profusely, and in which the tillers are frequently as tall as the main stalk. Since tillering is associated with productiveness in early maturing varieties (cf. Jones et al 1935), it is quite possible that the spread of maize to the region now the Northern United States was the direct outcome of the development, in the Pueblo region, of new, freely-tillering types resulting from an additional infusion of Tripsacum germplasm. Before this had occurred, however, it is probable that the Mexican dents were being pushed gradually farther and farther north through the slow process of acclimatization, so that the spread of the Southwestern types merely brought about rather suddenly the introduction of maize into the northern latitudes, a process which would otherwise have occurred only very gradually.

In any event, the spread of corn to the Northern Indian tribes must have been a comparatively recent event in terms of the period of time during which the Indians had occupied the country. Almost all the tribes had traditions of receiving agriculture and maize from elsewhere, and there is a decided resemblance among the various tribes in their names for corn. Will and Hyde (1917) estimate that the Mandans had practiced agriculture in the upper Missouri for only about 300 years previous to the European explorations of that region. Agriculture in the region now the Northern United States had not yet become a stable enterprise and was extensively supplemented by hunting and fishing, and most of the tribes were still in a stage of transition when America was discovered.

Perhaps the Norsemen who explored the eastern coast of North America in the tenth and eleventh centuries failed to mention maize in their sagas because it had not yet reached that region. There is still some controversy with regard to the southern limit of the travels of these intrepid explorers. Fernald (1910) has presented some convincing botanical evidence which indicates that they went no farther south than Labrador, while Gathorne-Hardy's (1921) more recent treatise includes some equally convincing evidence that they reached Long Island Sound. In any case they encountered only savage peoples and apparently did not see maize. If the thesis for southern migration could be definitely established, it would furnish rather convincing evidence that the New England Indians had not yet received corn at the time of the Norse explorations in the tenth and eleventh centuries. Such evidence, furthermore, would be in agreement with evidence from corn varieties, for the long, slender, straight-rowed flints of the Northeastern tribes are certainly a very recent development.

But this much is certain. By the time that Columbus and later European explorers began to reach American shores, maize was universally grown wherever agriculture was practiced from Canada to Patagonia. Many a time it was Indian corn that saved the early English settlers from starvation, and as Parker (1910) has so aptly stated, "And thus it is that the maize plant was the bridge over which English civilization crept, tremblingly and uncertainly, at first, then boldly and surely to a foothold and a permanent occupation of America."

CONCLUSIONS

We may, from the evidence now at hand, supplemented by a judicious use of the imagination, visualize maize as a wild pod corn originating from a remote Andropogonaceous ancestor which gave rise on the South American continent to a single species *Zea mays*, on the North American continent to a more variable genus, Tripsacum. Our knowledge of the Old World genera of related grasses—probably stemming from the same source and including Sorghum and Saccharum—is far from satisfactory, and the problem is one which merits much additional study. For America, however, the picture is reasonably clear. Both Zea and Tripsacum proceeded along parallel evolutionary paths so far as monoecism is concerned, both exhibiting a tendency to separate the sexes and to concentrate the staminate flowers in the terminal inflorescences and the pistillate flowers in the lateral ones. But here the similarity ends, for while Zea confined itself to, or became reduced to, a single species and remained a plant with low chromosome numbers and an annual habit of growth, devoting most of its energy to reproduction by seed, Tripsacum became a freely speciating genus, increased its chromosome number, assumed a perennial habit, and began to devote much of its energy to survival by the storage of food materials in the roots. Maize became more and more restricted in its range and was confined to extremely favorable sites scattered through the tropical forests, and was, indeed, probably on the road to complete extinction when man appeared on the scene; Tripsacum, in contrast, continued to spread until it had invaded regions formerly occupied by continental ice-sheets.

This was the situation when the Asiatic migrations to America began some ten to twenty-five thousand years or more ago. Propelled by the pressure of population in Northeastern Asia or perhaps only by the insatiable curiosity which is his Simian heritage, Neolithic, or perhaps Paleolithic, man traversed the gap between the eastern and western continents at, or near, Bering Strait, and began his long trek southward.

We suspect that the spread of man over the new continent was very similar to the spread of an insect or a weed introduced into a new region; perhaps like the boll-weevil which moved eastward from Mexico at an almost uniform rate of 40-50 miles per year, man moved southward at a random but more or less uniform rate, existing always, however, as a nomadic hunter and fisher, leaving behind him material evidence of his skill in the exquisitely fashioned Folsom points found in the Southwest, associated with the remains of a species of bison now extinct.

There was no agriculture in those early periods. Agriculture had not yet been invented in the Old World and man brought with him no agricultural traditions and none of the Old World crop plants. There was no incentive to invent agriculture in North America, for game and fish were reasonably abundant and, indeed, there were few native plants suitable for domestication. Not until he reached the lowlands of South America, and this may have been only a relatively short time after his arrival, a few thousand years at most, did he meet a combination of circumstances which induced him to adopt a new mode of life. Here he encountered a scarcity of game animals, counterbalanced by an abundance of excellent food plants, including mandioc, sweet potatoes, maize, and others. His first attempts at agriculture probably were confined to the root crops, for the operation of digging a root is so similar to that of planting one that no great amount of ingenuity is required to pass from one to the other, and man would be inclined to use the same pointed, fire-hardened "digger" stick for both. Once the planting of root crops had been learned, it was but another step to the planting of seeds, and at this point maize entered the agricultural complex. Originally regarded as an inferior source of food, because of its small, hard, and stony seeds, which were completely enclosed in the protecting glumes, the real value of the wild pod corn was not recognized until the accidental application of heat caused the seeds to burst from their enveloping glumes and converted the flinty endosperm to an easily masticated and palatable food.

The agriculture of the lowlands remained of a migratory sort and probably had no revolutionary effect upon the cultural development of those who practiced it. But as some of the more enterprising aborigines began to find their way up the numerous valleys of the adjoining Andean slopes searching for friable, alluvial soils free from competing forest vegetation, a marked change took place in the Asiatic savage who had drifted into South America. Here in the Andean region man's movements were decidedly restricted by the geographical features and a nomadic hunting life supplemented by a migratory agriculture was no longer possible. He became, of necessity, more proficient in the practice of agriculture, gradually adding new plants to his list of crops and learning to remove competing plants or weeds from the vicinity of those which he wished later to harvest for food. The pursuit of these labors gave him for the first time a stable food supply; and freed from the necessity of constantly searching for his next meal, he found leisure on his hands, which he began to devote to pottery-making, weaving, wood- and bone-carving, and the other activities which constitute the archaic level of culture. Under conditions such as those which exist in the Andean valleys this step was almost inevitable. Given a stable food supply, leisure, a stimulating climate, neither so hot as to sap man's vitality, nor so cold as to usurp all of his energy in the mere test of keeping alive, the development of a culture and finally a civilization is almost inevitable. And so there blossomed in the Andean region three highly advanced indigenous cultures which were later merged into the great Inca civilization.

After man had become more skillful in the practice of agriculture and had learned to restrain the competing weeds, maize became his most important crop plant. Even with its small seeds completely enclosed in glumes, it was by far the best cereal plant available in North or South America, and when the mutation from pod corn to naked corn occurred it soon became an even better one, for this mutation brought many other changes in its wake. The reduction of the glumes to inconspicuous scales or bracts, a change which had made the plant so much more useful to man, had also made it more susceptible to the depredations of insects and birds. The result was that when an occasional variation in the shortening of the lateral axis or an increase in the length of the leaf sheaths, or both, provided a partial protection for the naked seeds, selection, either direct human selection, or natural selection operating in a man-made environment, tended to favor the long sheathed variations; until a point was reached wherein the lateral inflorescence was completely enclosed by the husks as we know them today. There is no way of determining when and where the mutation from pod corn to naked corn first occurred. The mutation is one which may have occurred repeatedly in the past only to be lost in nature, but once it occurred under cultivation the primitive farmer, ignorant and inexperienced though he may have been in the art of plant breeding, recognized the value of a naked-seeded maize and began to propagate the new form. This may have occurred first in the lowlands or it may have occurred only after maize had been carried into the Andean region. In either case, however, we can be reasonably certain that the podded characteristic survived for a long period of time as a rogue in domesticated varieties. Later there must have been a tendency to propagate only the naked corn but even under these conditions the podded type may have survived for a long period, partly because it was capable of volunteering, partly because the podded gene was transmitted through the pollen and thus survived even when no podded seed was planted, and perhaps partly because occasionally the maize which had been stored for next year's planting was so injured by insects that only the protected pod corn remained for seed. In any case pod corn was sufficiently common that at least one representation of it has come down to us in the Peruvian pottery. Finally, however, the frequency of the podded gene in the population became so low and the Andean people had become such experienced agriculturists that a few generations of human selection removed the gene completely from the maize population of that region until today it is no longer in existence there and the natives have no name for it.

In the meantime, however, maize comprising a mixture of naked and podded types was adopted by less experienced agricultural tribes who have permitted the character to persist as a mixture in maize varieties until today.

During all of this period there was a rather free exchange of products between the Andean region and the adjoining South American lowlands, but there seems to have been but little intercourse between these two regions and Central America. Eventually, however, some of the lowland crops—including maize, mandioc, sweet potatoes, peanuts, peppers, and tobacco—spread into Central America and Mexico, where they were undoubtedly important factors in the development of the Maya and Aztec civilizations.

There is a possibility—at least the subject is one which merits serious investigation—that a fairly well developed agriculture with beans and squashes as a basis was already in existence in parts of Mexico and Central America when maize and the other South American lowland crops were introduced. The beans, squashes, cotton, and several other crops of this region are quite distinct from those of the Andean region. Wild species of these crops are indigenous in Mexico and Central America, and conditions for agriculture are favorable. It is not inconceivable, therefore, that agriculture had already been invented in this region before the South American lowland crops were introduced, and that the introduction of these very productive food plants to a people already experienced in agriculture was responsible, in part at least, for the sudden flowering of the Maya civilization and for its phenomenal development in a relatively short period of time.

In Central America for the first time since the two genera had become separated in remote geologic periods Zea and Tripsacum came into contact with each other on an extensive scale. They had become so divergent that hybridization was difficult; but at some time, the date of which it may be possible to determine when the botanical and archaeological evidence has been completely correlated, the opportunities for crossing of maize and Tripsacum became so great that at least one hybrid occurred. This hybrid, by repeatedly backcrossing with maize, resulted in the transfer of four fairly large segments of chromatin and perhaps several additional smaller ones from Tripsacum to Zea and the production of a new maize-like plant with two of the essential characteristics of Tripsacum—a covered seed and brittle rachis, characters which enabled it to survive in the wild. This new plant—later to be known as a separate genus, Euchlaena—did not spread rapidly and remained the dominant species only in a very limited area in western Guatemala. Being very closely related to maize, and in fact identical with maize except for the chromatin segments received from Tripsacum, Euchlaena hybridized freely with maize. Natural hybrids were sometimes carried north with the corn and a recombination of the translocation segments gave rise to new, more maize-like types of Euchlaena in various parts of Mexico. In this process some of the genes from Tripsacum were lost so that the new teosinte-like segregates were not as well adapted to survival in the wild as the original Euchlaena, but were able to persist as weeds in and around the corn fields.

The original hybridization of Zea and Tripsacum and later repeated hybridization of the new genus, Euchlaena, with its maize parent resulted also in the transfer of some Tripsacum genes to the genetic complex of cultivated maize. This gave rise to some new types of corn previously not in existence, including the North American pointed pop corns, the dent corns, and the long, slender, straight-rowed flint and flour corns, types which are not represented in the Peruvian pottery and which even today are still almost unknown in the Andean region.

Thus the great diversity of maize finally becomes explicable. For to the enormous diversity resulting from a long period of domestication in the Andean region where numerous samples of the original germplasm were isolated by physical barriers, there has been added, in Central America, further diversity resulting from hybridization with another genus.

The next great center of dispersal of maize after the Central American-Mexican region was the Southwestern United States. Here, in the same general region where Folsom man had roamed as a nomadic hunter, there developed the advanced culture of the Cliff-Dweller. There were undoubtedly many factors involved in the great differences between these two cultures which arose in the same region but one of the most important factors was certainly maize. Folsom man had never seen this plant; the Cliff-Dweller was dependent upon it for his existence.

From this center of dispersal, maize moved northward and eastward and was quickly adopted by many tribes who were beginning to feel the pressure of population upon the natural food supply of game and fish. It reached the Northern and Eastern tribes so recently, however, that the transition from a nomadic hunting life to a sedentary agricultural existence had not been completed when America was discovered, and most of these tribes were still living by a combination of the two activities. One wonders what a magnificent civilization might have been reared in the stimulating climate of the region now the Northern and Northeastern United States if the discovery of America had been delayed a few thousand years and the Indians in this region had been granted an opportunity to allow the impact of the recently acquired maize to achieve its full effects.

While the new types of corn were migrating northward and eastward from Mexico, some of them, particularly the hard-seeded flints, were also moving southward into South America where, except in the Andean region, they replaced almost completely the varieties previously grown.

As a consequence, the corn now grown in nearly all parts of North and South America shows evidence of contamination with Tripsacum in a number of characteristics, particularly in the presence of knobs on the chromosomes. The corn of the Andean region, however, still possesses knobless chromosomes. A realization of the importance of Tripsacum genes in the germplasm of most American corn varieties should lead to more intelligent methods of maize improvement.

This account of the origin and spread of corn is based in part upon substantial evidence, in part only upon the fact that more pieces of the puzzle can be satisfactorily fitted into this particular arrangement than in any other so far proposed. It accounts, we believe, for all of the facts now at our disposal. Although it differs in many respects from all of the hypotheses previously considered, it embraces important conclusions of almost every student who has ever approached the problem. The assumptions of Hackel, Iltis, and others that maize stemmed from an Andropogonaceous plant is supported by the evidence that modern maize originated from pod corn which was, in many ways, a typical Andropogonaceous plant. The emphasis that Sturtevant, Collins, and others placed upon the primitive characteristics of pod corn was evidently justified. The opinion of Harshberger, Kuwada, Collins, Arber, and others that corn is a hybrid is verified so far as all varieties except those from the Andean region are concerned. East's contention that teosinte is no more than a variation of maize is supported by the evidence. Sturtevant's opinion that pop corn is a primitive type and that the Cuzco corn of Peru represents the most highly domesticated type now seems to be sound. The theory of Montgomery and Weatherwax that Zea, Euchlaena, and Tripsacum represent the products of independent lines of descent from a remote common ancestor appears now to be valid for two of the three plants considered.

It is evident, therefore, that our own conclusions are, for the most part, not new. If we have made any contribution toward the solution of the problem, it has been primarily one of realigning the parts of a puzzle so that many which previously failed to fit have now fallen into place to present a picture which, though far from clear and revealing because many segments are still missing, is at least visible in outline and is suggestive of many new points of experimental attack on the problem.

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